EVALUATING PREDATORY CONTROL OF DENSE, SLOW-GROWING WHITE CRAPPIE USING HYBRID SAUGEYE

By

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Bachelor of Science: Animal Ecology

Iowa State University

Ames, Iowa

2015

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 2017

EVALUATING PREDATORY CONTROL OF

DENSE, SLOW-GROWING WHITE CRAPPIE

USING HYBRID SAUGEYE

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ACKNOWLEDGEMENTS

I would first like to thank my adviser, Dan Shoup, as well as my committee members Jim Long and Barney Luttbeg for advice and assistance writing this thesis. I would also like to acknowledge and thank employees of the Oklahoma Department of Wildlife Conservation (Ryan Ryswyk, Cliff Sager, Richard Snow, Matt Mauck, Ashley Nealis, Clayton Porter, John Perry, David Routledge, Shelby Jeter, Chandler Pettit, Joseph Whitman, and Tanner McAdams) and Oklahoma State University (Alexis Whiles, Blake Crispin, Garrett Johnson, John Dattilo, Jeff Johnson, and Sam Mosle) for their help with field sampling. This project would not have been possible without the collaborative efforts of the aforementioned. I also thank the Arkansas Game and Fish Commission for use of a long-term cove rotenone sampling dataset and Oklahoma Department of Wildlife Conservation for use of a long-term fyke net dataset. This work was supported by the USDA National Institute of Food and Agriculture Hatch project no 1006561 and the Division of Agricultural Sciences and Natural Resources at Oklahoma State University; and Sportfish Restoration Project number F-98-R administered by the Oklahoma Department of Wildlife Conservation.

Name: DRAY CARL

Date of Degree: MAY, 2018

Title of Study: EVALUATING PREDATORY CONTROL OF DENSE, SLOW-GROWING WHITE CRAPPIE USING HYBRID SAUGEYE

Major Field: NATURAL RECOURCES ECOLOGY AND MANAGMENT

Abstract: White Crappie *Pomoxis annularis* is an important sportfish throughout the U.S., but this species notoriously forms "stunted" (high-density, slow-growth) populations. Fishery managers have used a predatory-control strategy of stocking saugeye *Sander vitreum x Sander canadense* in an attempt to help improve crappie population size structure for anglers seeking larger crappie for recreation or harvest. Saugeye are hypothesized to consume small White Crappie thereby directly reducing crappie population density, indirectly relieving intraspecific competition within the population, and ultimately improving individual crappie growth rates. However, among Oklahoma reservoirs, this management strategy has not consistently improved White Crappie population size structure. Therefore, my research evaluated the overall ability of saugeye introductions to improve growth and size structure of White Crappie populations and evaluated biological mechanisms that might explain variation in management outcomes. I combined White Crappie samples from saugeye-stocked and unstocked lakes in a before-after-control-impact (BACI) design and found that stocked lakes had significantly larger increases in White Crappie size structure and growth than control lakes. However, variation of population demographics increased after saugeye stockings, suggesting some lakes responded better than others. Therefore, I conducted a saugeye diet study (six Oklahoma reservoirs), which revealed saugeye diets varied among lakes, seasons, and saugeye sizes, with consumption of crappie as high as 20-40% by weight for large saugeye (> 460 mm) in summer or fall in some lakes. This observed lake-to-lake variation in saugeye consumption of White Crappie may explain the variable efficacy of this management strategy. I integrated crappie consumption rates from saugeye bioenergetics models into White Crappie population models to explore the biological mechanisms underlying the predatory-control strategy. Predation mortality focused on a narrow range of crappie lengths, and therefore had large population-level effects on White Crappie biomass and growth. Size structure of White Crappie populations was dependent on initial population densities and mortality, and my models fit observed field data well. Overall, growth and size structure improvements were greatest in systems with high initial White Crappie densities, but improvements also had limitations, as biotic interactions are not the only factors shaping White Crappie population dynamics in southern reservoirs.

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CHAPTER I

EXTENDED ABSTRACT

White Crappie *Pomoxis annularis* is an important sportfish sought by anglers across the United States, but this species notoriously forms "stunted" (high-density, slow-growth) populations in Oklahoma (Mitzner 1984; Boxrucker and Irwin 2002), which can be undesirable to anglers seeking large crappie for harvest and recreation (Miranda and Dorr 2000). Managers and researchers have attempted several strategies to improve population size structure of stunted White Crappie in Oklahoma and southern reservoirs with little success (e.g., prey stockings, harvest regulations; Noble 1981; Hale 1996; Boxrucker 2002b). However, a saugeye *Sander vitreum x Sander canadense* stocking program was successful as a predatory-control of over-abundant White Crappie, increasing crappie growth and size structure in Thunderbird Reservoir, Oklahoma (Boxrucker 2002a). This success lead to increased stocking of saugeye as a predatory-control of stunted crappie populations.

Saugeye introductions have been common throughout Oklahoma (55 lakes stocked at least once since 1985) and numerous other southern reservoirs (e.g., Arkansas, Kansas) or

for predatory-control of White Crappie, with mixed results relative to improving White Crappie population size (Ryan Ryswyk and Cliff Sager, Oklahoma Department of Wildlife Conservation [ODWC], personal communication). This management strategy is dependent on saugeye directly consuming enough crappie to reduce population density, indirectly relieving intraspecific competition within the population, and ultimately improving individual crappie growth rates (Boxrucker 2002a; Galinat et al. 2002). Saugeye are both managed and advertised with regard to top-down control of White Crappie in most Oklahoma reservoirs; however, some ODWC fishery biologists have expressed concerns over the observed lack of efficacy of this management strategy in some lakes, and further research is needed to effectively evaluate this strategy.

I developed my thesis to evaluate the overall ability of saugeye introductions to improve growth and size structure of White Crappie populations and evaluate biological mechanisms that might explain variation in management outcomes from saugeye stockings. My research incorporated a combined approach of data mining historical samples (Chapter 2), field-based data collection (Chapter 3), and scenario-based modeling strategies (Chapter 4) to holistically address the potential utility of predatory-control of White Crappie by saugeye. With this comprehensive approach, study-specific questions built on one another throughout chapters, producing better interpretation and more refined understanding of results within each chapter.

The objective of chapter two was to compare changes in White Crappie population characteristics in lakes stocked with saugeye with changes that may have occurred in reference lakes that were not stocked with saugeye. An omission in past evaluation of this management strategy was failure to monitor control populations (no saugeye stockings) to distinguish changes in White Crappie populations due to saugeye from background variation (Maceina 2003; Pope et al. 2004; Brown et al. 2012). I gained insight into the overall effectiveness of this management strategy by combining stocked (impact) and unstocked (control) lakes in a before-after impact-control (BACI) design and teasing out these potential sources of variation (saugeye influence vs. non-saugeye influence). This study found saugeye-stocked lakes had significantly larger White Crappie PSD and mean length at age 2, but changes in PSD-P, W_r, CPUE, or mean length at age-1 were not significantly different than what occurred over the same time period in unstocked lakes. Several metrics had increased variation after saugeye stockings, suggesting some lakes responded more strongly than others, so saugeye stockings for improving White Crappie size structure may not work equally well in all systems.

Saugeye may not eat as much crappie in some lakes as others, potentially driving the variability in White Crappie responses to saugeye introductions observed by fishery biologists and results from chapter two. No comprehensive studies of saugeye feeding ecology exist, and investigating feeding ecology of saugeye in southern reservoirs is essential for predicting effects of saugeye introductions on White Crappie and other components of fish communities. Specifically, in chapter three I explored lake-, seasonal-, and size-related variation in diets, population-level niche width and individual

specialization, and trends in prey size of saugeye using diet samples from six Oklahoma reservoirs. I found White Crappie are not the dominant diet item for most saugeye, and smaller saugeye (≤ 460 mm TL) almost never eat White Crappie. However, consumption of White Crappie can be as high as 20-40% by weight for large saugeye (> 460 mm TL) in summer or fall in some lakes.

The previous evaluation of this management strategy (Boxrucker 2002a) and chapter two indirectly estimated influences of saugeye introductions on White Crappie populations, but did not evaluate the actual mechanisms that determine its effectiveness. Therefore, the purpose of chapter four was to directly model the influence of introducing saugeye predation on Oklahoma White Crappie population biomass, growth, and size structure to determine strength of saugeye influence on White Crappie under different conditions. I combined crappie consumption estimates from population-level saugeye bioenergetics model (fit to data from Oklahoma reservoirs) with an age-based White Crappie population model using field data and diet data from chapter three. This study was designed to help disentangle the mechanisms (e.g., density-dependent growth, size-specific mortalities, etc.) underlying this predatory-control strategy and shed light on situations where it will be most and least successful. I found most saugeye populations do not consume large amounts of crappie, but predation mortality was focused on a narrow range of crappie lengths and had large population-level effects on crappie biomass and growth. Size structure of White Crappie populations was dependent on initial densities, mortality, and increases in growth from density-dependent feedbacks, and my models fit observed field data relatively well.

The following chapters are written as individual studies to be published as separately. Together, these three studies illustrate a more complete picture of a predatory-control management strategy for crappie to date by using a combined effort of data mining, field data collection, and modeling. I conclude that saugeye stockings can be useful in improving White Crappie size structure, but the degree of effectiveness will vary among systems, in part depending on the size of the White Crappie population, the density of saugeye established by stockings, and the degree to which saugeye eat White Crappie. Growth and size structure improvements are expected to be greatest in systems with high initial White Crappie density, but improvements also have limitations, as density-dependent processes and biotic interactions are not the only factors shaping White Crappie population dynamics in southern reservoirs.

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CHAPTER II

REEVALUATING WHITE CRAPPIE POPULATION RESPONSES TO SAUGEYE INTRODUCTIONS

Introduction

High densities of fish often result in slower growth rates within a population and ultimately lead to suboptimal population size structure (Headley and Lauer 2008; Lorenzen 2008), which can be undesirable to anglers pursuing larger individuals of sportfish populations (Isermann and Paukert 2010). These slow-growing populations may develop from factors such as limited prey availability (Mittelbach 1988), habitat displacement (Abrams 1986), or lack of a top predator (Mitzner 1984), which lead to high population density. High densities can ultimately cause increased intraspecific competition and reduced individual growth rates through density-dependent feedbacks (Lorenzen 2008). This density-dependent growth relationship commonly occurs in several small-bodied sportfish species (Heath and Roff 1987; Ridgway and Chapleau 1994), and can propose problems to fishery managers interested in improving size structure of fisheries.

Crappie *Pomoxis* spp. are important small-bodied sportfish sought by anglers across the United States that notoriously form stunted populations (Mitzner 1984; Boxrucker and Irwin 2002). As a result, researchers have attempted several management strategies to increase centrarchid growth rates including prey stockings (Devries and Stein 1990; Hale 1996) and habitat alterations (Olson et al. 1998) with varying results. High-density, slow-growth fish populations are hypothetically well-suited to protected slot limits (Isermann and Paukert 2010) where harvest of small individuals is encouraged to reduce population density and intraspecific competition. However, anglers typically do not harvest small crappie, so a slot limit would likely be ineffective. Mechanical or chemical removal of small crappie could also be helpful, but is both time and cost inefficient (Mitzner 1984). Thus, Willis et al. (1984) proposed that predatory control (increased biomass of predator species) could be the most effective way to reduce small crappie densities. Predators can directly control abundances of prey populations (Irwin et al. 2003; Weidel et al. 2007) and indirectly control growth rates and population size structure via density-dependent growth mechanisms (Guy and Willis 1990). Further, predatory control of prey populations has been observed with numerous piscivorous species, including Walleye *Sander vitreum* (Hartman and Margraf 1993; Ivan et al. 2011), and management strategies aimed at increasing predator densities to manipulate prey abundances are common (Isermann and Paukert 2010).

Saugeye *Sander vitreum x Sander canadense* have been introduced into multiple reservoirs as a predatory control for dense crappie populations (Boxrucker 2002; Galinat et al 2002). For example, 55 Oklahoma lakes have been stocked at least once with

saugeye since 1985 (Oklahoma Department of Wildlife Conservation [ODWC], unpublished data). Significant increases in mean length at age, relative weight, and proportion of quality-size White Crappie *Pomoxis annularis* in Thunderbird Reservoir, Oklahoma were attributed to the introduction of saugeye (Boxrucker 2002). Similar responses in the mid-1990's were observed in Black Crappie *Pomoxis nigromaculatus* population size structure and mean length at age in Lake Richmond, South Dakota (Galinat et al. 2002). These evaluations suggest saugeye may effectively reduce competition among small crappie. However, many saugeye stockings in Oklahoma have failed to improve White Crappie size structure (Ryan Ryswyk and Cliff Sager, ODWC, personal communication), and mechanisms explaining success of this management strategy need evaluated to explain differing results.

Previous studies of predatory control for thinning crappie populations suffer from multiple shortcomings. First, environmental influences on crappie recruitment (Mitzner 1991; Maceina 2003) or growth (Beam 1983; Pope et al. 2004) may account for changes in crappie population characteristics independent of saugeye introductions. Second, different fish communities can have varying responses to perturbations (Tunney et al. 2017), suggesting all reservoirs may not respond similarly to saugeye introductions. These issues can be addressed with a study that includes multiple lakes (Hansen et al. 2007) and monitors control lakes (no treatment) in the same time frame (Brown et al. 2012) to help differentiate trends in population metrics from potential random or natural variation. The objective of this study was to compare White Crappie size structure, condition, abundance, and growth before and after saugeye introductions in multiple

reservoirs with reference lakes (systems not stocked with saugeye) in a before-after-control-impact (BACI) analysis of variance design. Results of this study will act to 1) test if saugeye stocking improves population characteristics of over-abundant White Crappie and 2) assess whether saugeye stocking can improve White Crappie population characteristics to the level of quality fisheries (reference lakes).

Methods

I used historic standardized sampling data from the ODWC to evaluate changes in White Crappie population size structure (proportional size distribution [PSD and PSD-P]; Guy et al. 2007), condition (mean relative weight [Wr]; Neumann et al. 2012), abundance (catch-per-unit-effort [CPUE]), and growth (mean length at age 1 and 2) related to saugeye stockings using a BACI experimental design (Stewart-Oaten et al. 1986). Condition was evaluated because relative weight may act as an indicator of competition within the population (Neumann et al. 2012), and size structure was evaluated for potential effects on the White Crappie fishery in a management context. Lakes selected as either impact (stocked with saugeye) or reference (never stocked with saugeye) were required to have at least one annual fyke net sample with $\geq$25 White Crappie before and after the year of saugeye introduction. The year of saugeye introduction was defined as the year at which saugeye were first observed in ODWC Standard Sampling Procedure boat electrofishing samples, indicating survival of stocked fish through first summer after stocking.

BACI analyses are used to evaluate how a treatment affects sites through time compared to reference (no treatment) sites over the same time frame (Conquest 2000; Stewart-Oaten and Bence 2001). It is not necessary for reference sites to be have the same initial values as treatment sites (Stewart-Oaten et al. 1986; Conquest 2000; Smokorowski and Randall 2017) because the BACI design explicitly accounts for initial differences that might exist between treatment and reference sites and look for parallel (no interaction) or orthogonal (significant interaction) responses between treatment and reference sites across time. Each impact lake (stocked with saugeye) in my study was paired with a reference lake (not stocked with saugeye) based on similar lake morphometry to establish the transition year (before to after) for each reference lake (Figure 1); however lakes were not actually paired in statistical analyses (i.e., all reference lakes were simply treated as replicate reference systems). Data from reference lakes with similar "stunted" White Crappie populations as impact lakes were not available, so reference lakes represented "quality" fisheries and were also used as a standard for evaluating whether saugeye stocking could create quality White Crappie fisheries. Reference lakes had one of two White Crappie length regulations in Oklahoma lakes (statewide [no size limit; N=3] and 10-inch minimum length limit [N=3]). *Ad hoc* BACI tests showed that within the six reference populations, White Crappie population characteristics in lakes with statewide harvest regulations responded similarly (no significant interactions for any of the response variables) to those with minimum length regulations. All impact lakes had the statewide (no size limit) regulation.

Fyke net samples (ODWC Standard Sampling Procedure) were used to determine White Crappie population size structure, condition, and abundance throughout the study. In short, fyke nets (12.7-mm mesh, two 0.91-m X 1.83-m frames, four 0.76-m hoops, and a 20.12-m lead) were set perpendicular to the shoreline in fall when surface water temperatures were between 15.6 and 21.1°C. Individual White Crappie were typically measured to the nearest mm total length and weighed to the nearest g. However, in some cases additional White Crappie were sampled that were not weighed and were measured to the nearest 10-mm total length grouping. These additional White Crappie were only used for size structure and abundance metrics (i.e, not used for relative weight calculations).

I calculated proportional size distributions (PSD, PSD-P) as an index of White Crappie population size structure (Guy et al. 2007) and mean relative weight (W_r) as an index of condition (Blackwell et al. 2000; Pope and Kruse 2007). I calculated mean CPUE as an index of total crappie abundance, which was calculated as the mean of the total number of White Crappie per 24-hr net night for each net. Mean length at age 1 and 2 were chosen *a priori* as indices of White Crappie growth. A subsample of captured White Crappie had otoliths removed and ages estimated (between 20 and 30 fish per 25 mm group $\geq$ 120 mm). Ages were applied to all White Crappie within a given sample using smoothed age-length keys constructed with multinomial logistic regression (nnet package, Venables and Ripley 2002; Ogle 2016), and mean lengths were calculated for the age-1 and 2 cohorts.

White Crappie samples were categorized by time (before/after saugeye introduction) and treatment (impact/reference lake) and all samples up to 13 years prior to stocking or 19 years after establishment of saugeye were used. All indices were evaluated using separate BACI tests consisting of a two-way analysis of variance (ANOVA; time, treatment, and time * treatment interaction as fixed factors; lake as random factor) in Program R (lme4, Bates et al. 2015; R Core Team 2017) with alpha set at 0.05 *a priori*. I visually assessed all response variables for normality with normal Q-Q plots and tested for equal variances among grouping variables (time and treatment) for all response variables using Levene's tests (alpha = 0.05; car R package, Fox and Weisberg 2011). PSD values were square-root transformed, and PSD-P and CPUE values were log-transformed to meet ANOVA assumptions (normal distribution and homoscedasticity).

Results

Twelve lakes (Figure 1) were used in the BACI design. A total of 123 annual White Crappie samples (37 Pre, 86 Post) was used to evaluate PSD, PSD-P, and CPUE, and 121 samples (36 Pre, 85 Post) were used to evaluate mean relative weight. A total of 106 samples (32 Pre, 74 Post) was used to evaluate mean length at age 1, and 105 samples (31 Pre, 74 Post) were used to evaluate mean length at age 2. Mean number of individual fish per sample was 659 (SE = 161) per sample (lake/year combination). The year of saugeye introduction ranged from 1987 to 1995; the years of White Crappie fyke net samples used in the analysis ranged from 1980 to 2012. The observed interquartile range (IQR) for all six population metrics increased after saugeye introductions in the impact lakes (Figures 2, 3), suggesting metrics in some lakes improved more than other lakes creating an increase in variance of observed population metrics.

The interaction between time (before/after saugeye introduction) and treatment (impact/reference lake) was significant for PSD ($F_{1,110.5} = 6.12$, $P = 0.01$) and mean length at age 2 ($F_{1,93.6} = 10.04$, $P < 0.01$), indicating size structure and growth of impact reservoirs improved more than reference reservoirs after the time of saugeye introductions (Figures 2, 3). However, PSD-P ($F_{1,110.4} = 0.48$, $P = 0.49$), mean relative weight ($F_{1,109.4} = 1.27$, $P = 0.26$), CPUE ($F_{1,109.1} = 0.11$, $P = 0.75$), and mean length at age 1 ($F_{1,94.7} = 0.76$, $P = 0.39$; Figure 3) did not have significant interactions, indicating both impact and reference reservoirs responded similarly through time (Figures 2, 3). White Crappie PSD-P, mean relative weight, and mean length at age 1 significantly increased and CPUE significantly decreased in both stocked and unstocked lakes after

saugeye introduction (significant time effect; PSD-P, $F_{1,110.4} = 31.14$, $P < 0.01$; W_r, $F_{1,109.4} = 6.92$, $P < 0.01$; mean length at age 1, $F_{1,94.7} = 19.47$, $P < 0.01$; CPUE, $F_{1,109.1} = 15.42$, $P < 0.01$; Figures 2, 3). Impact lakes had significantly lower White Crappie PSD-P and mean length at age 1 (significant treatment effect; $F_{1,9.8} = 8.60$, $P = 0.02$; mean length at age 1, $F_{1,10.5} = 10.67$, $P < 0.01$; Figures 2, 3) both before and after saugeye introductions. There were no significant differences in condition or abundances between impact and reference lakes (CPUE, $F_{1,9.9} = 2.67$, $P = 0.13$; mean W_r, $F_{1,10.3} = 4.03$, $P = 0.07$; Figure 2).

Discussion

White Crappie size structure (PSD) and growth (mean length at age 2) improved more in lakes stocked with saugeye compared to reference lakes, suggesting predatory-control of high-density crappie populations is possible and can improve growth rates and population size structure. However, the other population metrics I evaluated (PSD-P, relative weight, CPUE, and mean length at age 1) had similar trends irrespective of saugeye stocking, suggesting the introduction of saugeye was unsuccessful at improving these metrics. These other metrics did change in reference lakes during the post-stocking era, so it is possible the changes in reference lakes masked changes related to saugeye stockings, but it is just as likely that these changes were the result of regional factors (possibly driven by environmental influences such as hydrology, temperature, etc.; Maceina 2003; Pope et al. 2004). Even so, none of the White Crappie population metrics from impact lakes improved to the level of standard “quality” crappie fisheries represented by the reference lakes, indicating saugeye stocking alone cannot improve

White Crappie growth and size structure to levels of reference lakes. This minimal level of improvement suggests that other factors besides density-dependent relationships also influence population dynamics of quality White Crappie populations (i.e. coarser-scale constraints such as geology or other environmental influences; Wiens 1989).

Saugeye introductions produced variable responses in White Crappie populations within impact lakes (i.e., IQR of measured metrics increased after saugeye stockings), likely adding to my inability to detect significant BACI interactions for some response variables. In reference lakes, the IQR only increased for one metric (mean W_r), so variability within impact lakes was likely not driven by weather or other temporal changes. Instead, increased variability within impact lakes may result from saugeye stockings that were more effective in altering White Crappie growth and size structure in some lakes than others. Direct modeling strategies would be best to fully understand the mechanisms underlying these patterns; however, several hypotheses could explain the apparent variation on treatment lake responses. For example, the proportion of crappie in the diets of saugeye vary among lakes in Oklahoma (2.2%-23.0% by weight; Chapter 2), making saugeye unlikely to affect crappie in lakes where crappie are rarely eaten by saugeye. Alternatively, differences in saugeye densities (i.e., variable stocking success) could directly influence predatory effects on White Crappie populations, where lakes with low saugeye recruitment would not meaningfully influence crappie. It is also possible that certain environmental influences present at only some lakes affected White Crappie more strongly than saugeye stockings, minimizing the impact of saugeye

stockings in some systems. Whatever the cause, it is clear that saugeye stockings produced stronger results in some systems than others.

Saugeye may not improve density-dependent growth of smaller, age-0 crappie, which could create limitations for improvement of crappie population size structure using predatory control. Most crappie consumed by saugeye are age-1 (Chapter 3), therefore saugeye may be unable to significantly affect size until age-2 because age-0 and age-1 abundances have not been sufficiently reduced to alter growth rates. Further, density dependence typically only occurs for younger ages (age 0-2) of White Crappie (Pope et al. 2004), so saugeye predation can only really improve size structure by improving growth at age 2 (with perhaps modest improvements to growth in age 1). The late age of White Crappie consumed by saugeye, and resulting late age at which density dependence is therefore relieved, may explain why I only observed improvements in PSD and not PSD-P as White Crappie may need higher growth throughout all ages to reach preferred size before end of life.

Initial differences between impact and reference lakes are accounted for with the BACI design, but other sources of variation (e.g., geological) among lakes could have also influenced results. Fishery researchers conducting field studies generally lack control over experimental units (e.g. lakes, fish), making it difficult, if not impossible, to perfectly design experiments with "identical" control treatments. However, without any comparison to reference populations, management-strategy evaluations are simply anecdotal case studies, the results of which could be erroneously influenced by temporal

changes caused by cyclical weather patterns (e.g., flood or drought years) or other coincidental temporal effects that are unrelated to the management action. Ideal controls were not available for evaluation in my study, but the inclusion of reference lakes still provided more information than would have occurred without them; specifically, the observed changes in PSD-P and CPUE that occurred within impact lakes also occurred in reference lakes, so these changes are as likely to be caused by regional patterns as they are saugeye stockings (differentiating the source of these changes is beyond the scope of this study). The BACI design is robust to initial differences between control and impact lakes because reference sites (controls) are not true controls in the traditional sense, but are only used to "control" (reduce) extraneous variation (Stewart-Oaten and Bence 2001). However, interpretation of BACI designs should be made with caution in cases with dissimilar controls as difference in lake potential must be considered (Smokorowski and Randall 2017). In my case, results should be interpreted with the understanding that reference lakes were moderate- to high-quality White Crappie fisheries, so reference lakes could have been closer to an upper limit for certain population metrics (e.g., PSD values near 100), potentially influencing results. Additionally, some reference lakes were located in different ecoregions than impact lakes, and coarser-scale constraints and associated environmental differences (e.g., differences in turbidity due to geology, etc.) may have different underlying effects on White Crappie population demographics. However, my results also clearly indicate that the average impact lake did not improve to the same level as these quality reference systems within Oklahoma, so saugeye stocking alone is unlikely to turn a poor crappie fishery into a quality one.

My study showed that introducing saugeye can improve population growth (mean length at age 2) and size structure (PSD) of White Crappie in Oklahoma reservoirs, however among-lake variation in White Crappie population responses indicated saugeye introductions produced greater improvements in some lakes than others. Further investigation of saugeye ecology (habitat use, movement, diets, etc.) in southern reservoirs would be beneficial in evaluating the dynamics behind the observed variation in effectiveness of predatory-control of White Crappie, but my results suggest the effects of saugeye introductions are at best moderate and this management technique is unlikely to move fishery metrics to the level of high-quality White Crappie fisheries. This observation may warrant changes in saugeye stocking effort, regulations, or advertising (i.e., reflecting the use of saugeye as a sportfish vs. a biological control) on a lake-by-lake basis in systems where control of over-abundant White Crappie is not realized.

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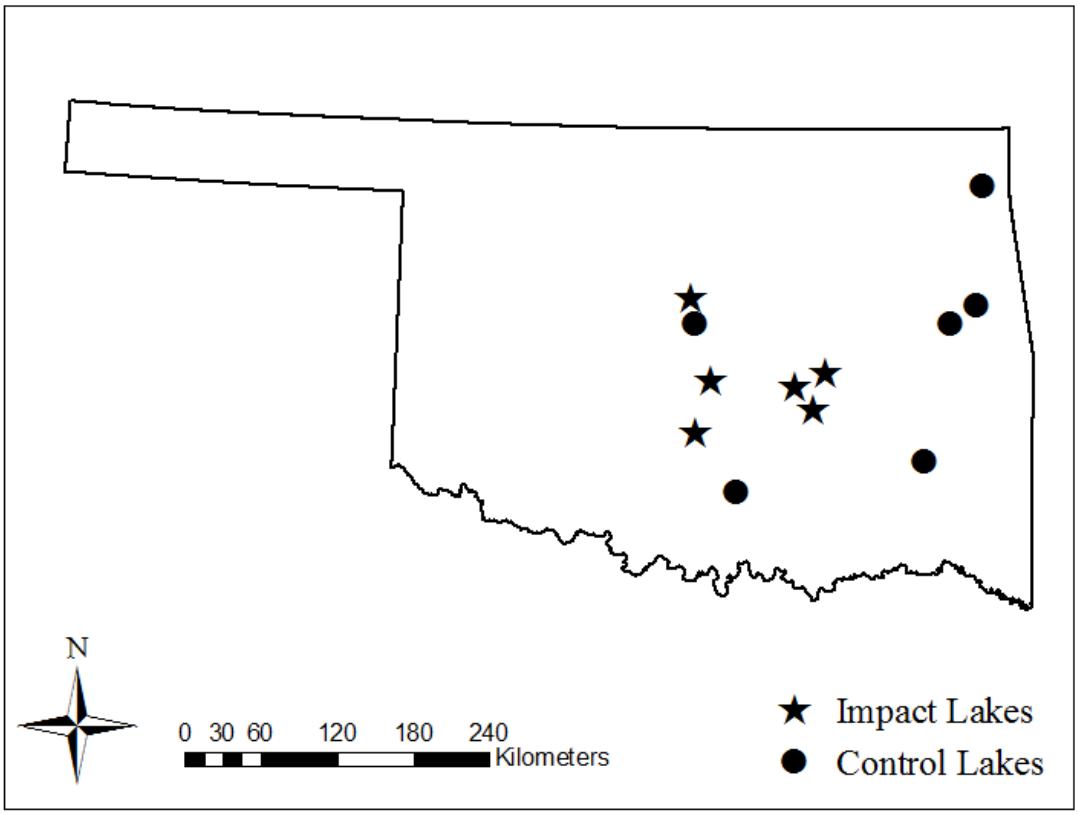

Figure 1. Lakes sampled to evaluate potential effects of saugeye introductions on White Crappie size structure, condition, abundance and growth. Impact lakes (received saugeye stockings) were Guthrie Lake, Wiley Post Lake, Thunderbird Reservoir, Wewoka Lake, Lake Holdenville, and Lake Wetumka (listed left to right) and paired control lakes (no saugeye stockings) were Arcadia Lake, Lake of the Arbuckles, Sardis Lake, Greenleaf Lake, Tenkiller Ferry Lake, and Grand Lake o' the Cherokees (listed left to right).

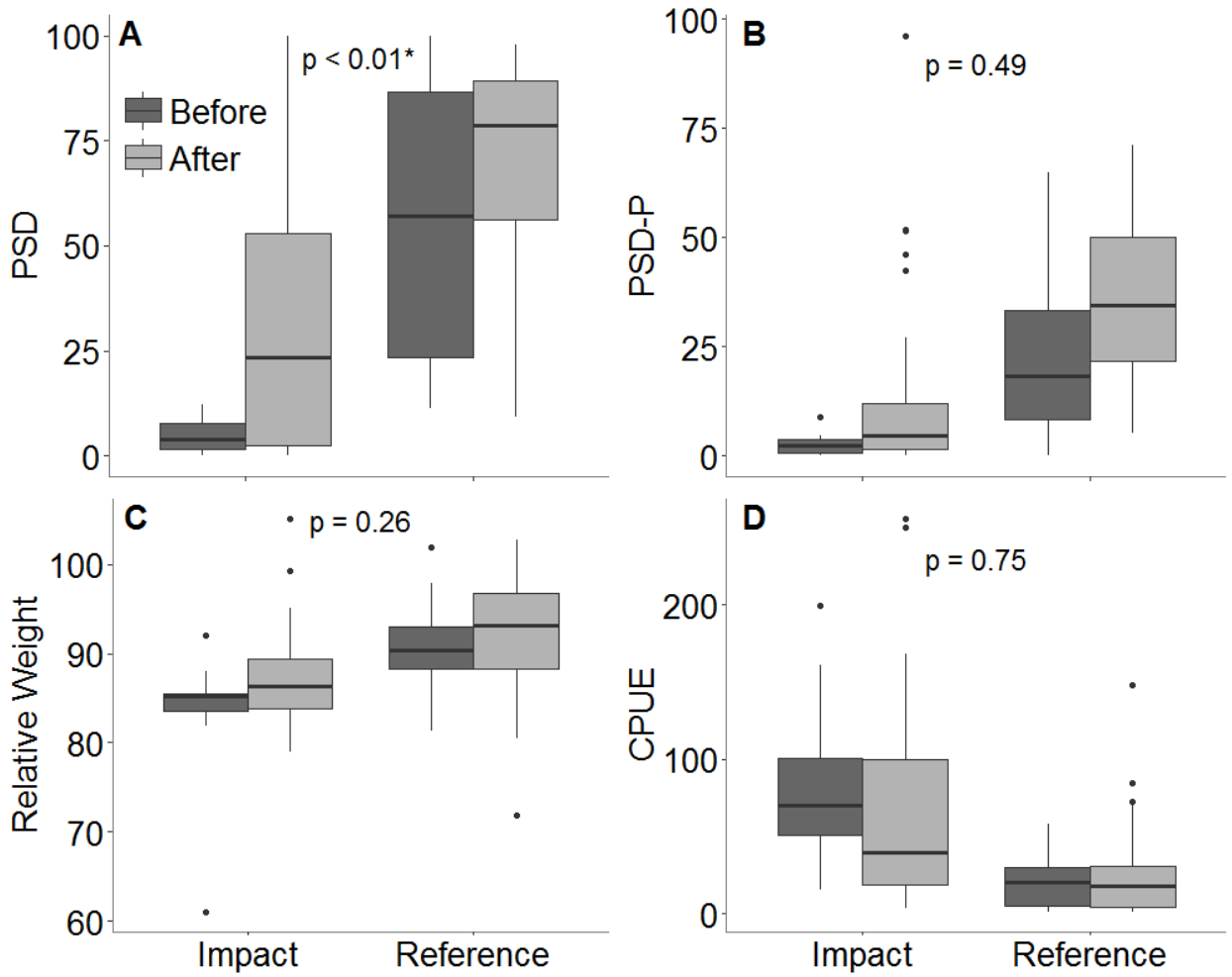

Figure 2. Boxplots comparing White Crappie population size structure (PSD [A], PSD-P [B]), mean relative weight (C), and abundance (D; CPUE) from before (dark grey) and after (light grey) saugeye introductions in both impact (stocked with saugeye) and reference (not stocked with saugeye) lakes. P-values are from the time*treatment ANOVA interaction, indicating whether impact and reference lakes responded similarly (insignificant interaction) or differently (significant interaction) through time. Thick lines indicate medians, boxes indicate the inner-quartile range [IQR], thin horizontal lines indicate reasonable extremes (+/- 1.58 times IQR/sqrt[n]), and dots indicate outliers.

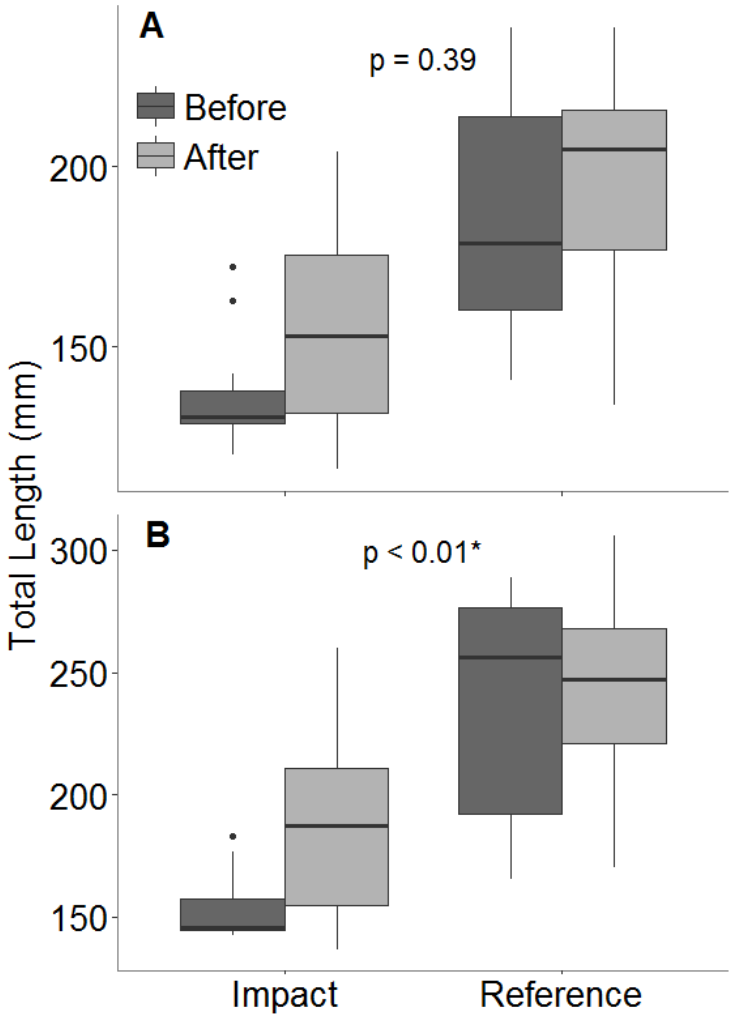

Figure 3. Boxplots comparing mean length at age for age-1 (A) and age-2 (B) White Crappie before (dark grey) and after (light grey) saugeye introductions in both impact (stocked with saugeye) and reference (not stocked with saugeye) lakes. P-values are from the time*treatment ANOVA interaction, indicating whether impact and reference lakes responded similarly (insignificant interaction) or differently (significant interaction) through time. Thick lines indicate medians, boxes indicate the inner-quartile range [IQR], thin horizontal lines indicate reasonable extremes (+/- 1.58 times IQR/sqrt[n]), and dots indicate outliers.

CHAPTER III

FEEDING ECOLOGY OF HYBRID SAUGEYE *SANDER VITREUM X SANDER CANADENSE* IN SOUTHERN RESERVOIRS

Introduction

Predator-prey interactions are crucial in shaping fish communities in nearly all aquatic ecosystems, particularly small, freshwater systems (Northcote 1988; Tonn et al. 1992). Predators can directly control abundance, growth, and other population characteristics in prey populations (Guy and Willis 1990; Santucci and Wahl 2003) as well as influence the life history strategies of their prey (Reznick et al. 1990). Predators can additionally produce non-consumptive effects on prey populations (i.e. prey behavioral responses), which can sometimes have a stronger influence than direct, consumptive effects (Preisser et al. 2005; Peckarsky et al. 2008). Manipulating piscivore abundances can sometimes even lead to trophic cascades and switching between alternative stable states in lakes (Perrow et al. 1997; Mehner et al. 2002). Ultimately, these top-down effects of predation are dependent on the feeding ecology of the predator population (Juanes et al. 2002), so it is important to understand predator feeding ecology in systems that are to be managed.

Piscivores can have diverse feeding ecologies due to specific adaptations of individual species and the different influences abiotic and biotic factors have on each piscivore (Mittelbach and Persson 1998; Juanes et al. 2002; Shoup and Wahl 2009). Many predator species differ in feeding behavior (e.g. stalking vs. ambush) or strategy (e.g. specialized vs. generalized) and may have different niche widths (Amundsen et al. 1996; Juanes et al. 2002). Morphological adaptations of predators (e.g. gape width, tooth development) and prey (e.g. spines, size) can also influence types and sizes of prey captured by predators(Hoyle and Keast 1987a; Wahl and Stein 1988). Further, feeding ecology within a single piscivorous species can vary seasonally (Sammons et al. 1994; Kocovsky and Carline 2001; Quist et al. 2002b), among populations (Vander Zanden et al. 2000), and among environmental conditions (Dionne and Folt 1991; Shoup and Wahl 2009; Shoup and Lane 2015). Primary piscivores generally undergo an ontogenetic shift to piscivory within the first weeks or months of life (Mittelbach and Persson 1998), which usually results in increased growth rates (Olson 1996). These ontogenetic diet shifts can also occur after the initial switch to piscivory as a fish grows in size and more prey types and sizes are available (Liao et al. 2002). Investigating the feeding ecology of predators is critical in predicting predatory effects on lower trophic levels and successfully managing predator-prey balance in lakes and reservoirs.

Saugeye *Sander vitreum x Sander canadense* is considered a "specialist piscivore" (Keast 1985), meaning it begins feeding on fish quickly after birth. Saugeye is a hybrid species created in hatcheries with a female Walleye *Sander vitreum* and male Sauger *Sander canadense* and has been introduced throughout the central U.S. to supplement declining

Walleye fisheries (Denlinger et al. 2006), introduce additional recreational fishing opportunities, and as a biomanipulation tool for improving over-abundant crappie *Pomoxis* spp. fisheries (Boxrucker 2002; Galinat et al. 2002). Like its parent species, saugeye is fusiform in shape, toothed, and is primarily a visual predator with a specialized light-gathering layer (*tapetum lucidum*) within the eye which allows it to see well in low-light conditions. However, saugeye displays faster growth rates (Siegwarth and Summerfelt 1990), higher thermal tolerances (Zweifel et al. 2010), and different habitat preferences (Johnson et al. 1988) than its parent species, suggesting saugeye may also exhibit different feeding habits. Few studies have addressed saugeye diets and feeding ecology in detail, especially at southern latitudes (Leeds 1988), and those that have are limited in scope to single lakes (Johnson et al. 1988). Given the frequency with which saugeye are stocked in reservoirs, it is important to understand the trophic relationships this management action may change, so more information is needed about the feeding ecology of saugeye.

The purpose of this study was to determine diet compositions of typical southern-latitude saugeye populations with a multi-scale study. Specifically I explored lake-, seasonal-, and size-related variation in diets, population-level niche width and degree of individual specialization, and trends in prey size consumed by saugeye in six Oklahoma lakes. Sampling multiple populations allowed us to examine lake-to-lake variation in saugeye diets and combine samples to evaluate saugeye feeding ecology across the region. Many hybrid and non-hybrid sportfish species (usually top predators) are stocked into water bodies without full knowledge of the associated feeding ecology and potential ecosystem

effects of the introduction ("stocking-up freshwater food webs"; Eby et al. 2006). The results of my study will provide managers and researchers with a better understanding of basic saugeye feeding ecology and is the first step in evaluating top-down effects of saugeye on lower trophic levels.

Methods

Diet collection

Six Oklahoma reservoirs with different sizes and habitat conditions were sampled for one continuous year each between 2015 and 2017 (Table 1). Saugeye diets were collected seasonally (based on observed surface water temperatures; spring: 10.0 – 21.1°C [mid-February – April], summer: >24.0°C [mid-June – August], and fall: 23.0 – 10.0°C [October – mid-December]; Walrath et al. 2015). Saugeye thermal tolerance is slightly higher than that of Walleye (Zweifel et al. 2010), and Walleye begin to seek thermal refuge at temperatures above 23°C (Ager 1976); so 23°C was used as the approximate summer transition temperature. A minimum of four sampling trips per season in each lake (mean = 6.9/season) was conducted. Saugeye were collected using boat-mounted electrofishing (60 pps DC generated by a 5.0 or 7.5 Smith-Root model GPP electrofishing system). Supplemental fish were collected using short experimental gill net sets (2 – 4 hrs; set parallel to shore using North American Standard gillnet design; Bonar et al. 2009) to help collect sufficient sample sizes of diets when electrofishing catch rates were low (Denlinger et al. 2006). Mean relative weight (W_r) and proportional

size distributions (PSD, PSD-P) were summarized from electrofishing samples for each lake (Guy et al. 2007; Pope and Kruse 2007; FSA R package, Ogle 2017).

All saugeye were measured (total length; mm) and weighed (g), and diet contents were collected using gastric lavage (Kamler and Pope 2001; Quist et al. 2002a). Small saugeye (< 330 mm) stomachs were flushed with a large syringe (150 mL) and vinyl tubing, and larger saugeye (> 330 mm) were flushed using a bilge pump and vinyl tubing (12.7 mm inside diameter). All diet contents were collected in a 500-micron wire-mesh sieve, rinsed into Whirl-Paks®, and preserved in 95% ethyl alcohol for later identification. Additionally, I dissected 52 stomachs of saugeye (229 – 634 mm; evenly distributed) after gastric lavage to validate efficiency of the technique.

Diet processing and analyses

Saugeye were divided into three PSD size categories (Gabelhouse 1984): preferred-size and larger [>460 mm]; quality [350 – 459 mm]; and stock [200 – 349 mm]) for ontogenetic diet comparisons. Lake Lawtonka did not have any stock-size fish because of a missing year class (this lake receives stockings every other year) and was not used in the analysis of stock-size diet analyses. Prey items were identified to species (or the lowest level possible given the state of digestion) and grouped into eight prey groups based on taxonomic and ecological similarities (Table 2; Chipps and Garvey 2007). All invertebrates were pooled into a general invertebrate prey group (Table 2) and were composed of Ephemeroptera, Odanata, Diptera, and Decapoda (in order of relative

frequency). Unidentifiable fish remains accounted for only 1.6% of recovered prey and were omitted from further analyses (Lipovsky and Simenstad 1978; Chipps and Garvey 2007). Each identifiable fish diet item was weighed (nearest 0.01 g).

I used several methods to explore saugeye feeding ecology and determine lake-, seasonal-, and size-related differences in diet compositions. Mean proportion by weight (MW_i) was calculated and used in most analyses to account for the energetic importance of various prey types (Bowen 1996). I integrated frequency of occurrence (total number of occurrences of a specific prey group / total number of full stomachs) and prey-specific abundance (proportion by weight from only those saugeye stomachs in which the particular prey group occurred) in a graphical technique modified by Amundsen et al. (1996) for each saugeye size category. These plots provide ecological insight into saugeye prey importance (diagonal from bottom-left [rare prey] to top-right [dominant prey]), feeding strategy (vertical axis; specialization on top, generalization on bottom), and niche width (diagonal from bottom-right [low degree of individual specialization] to top-left [high degree of specialization]) relative to saugeye size (Manko 2016).

Several multivariate assumptions make determining statistical differences among diet compositions inherently difficult (Chipps and Garvey 2007). Therefore, I built simple, two-way correspondence analysis (CA) plots (ca, FactoMineR, factoextra R packages; Nenadic and Greenacre 2007; Le et al. 2008; Kassambara and Mundt 2017) to graphically visualize trends and differences in MW_i among lakes, seasons, and saugeye

sizes (Jackson 1997; Chipps and Garvey 2007; Digby and Kempton 2012). Relative significance of each CA was evaluated using the sum of eigenvalues from the first two dimensions (included in CA plots). To interpret CA plots, the relative variance explained by each dimension are in parentheses of axis titles, and greater distances from the origin indicate stronger relationships. Additionally, small angles between arrows and prey items relative to the origin indicate strong, positive relationships between the arrow grouping and prey item, while 90° angles represent no relationship, and 180° angles indicate strong, negative relationships. Only prey groups with more than five occurrences within each respective saugeye size category were included in both bivariate and CA plots.

Investigating patterns of prey size consumption by saugeye may provide insight into the mechanisms that affect their diets. To quantify prey size, I reconstructed lengths of all fish prey (with the exception of samples from Thunderbird Reservoir) using linear relationships between backbone length and total length (derived from completely intact fish prey; Table 3) and total length and weight (linear relationship of log-transformed total length and weight; gathered from Fishbase or derived from completely intact prey items; Froese and Pauly 2017; Table 3). Reconstruction of prey lengths and weights is common in diet studies to eliminate biases caused by digestion (Trippel and Beamish 1987; Hansel et al. 1988; Scharf et al. 1997). I then fit quantile regressions (0.05, 0.50, 0.95; quantreg R package, Koenker 2017) representing the 5^{th} percentile, median, and 95^{th} percentile prey lengths (reconstructed total length; mm) relative to saugeye size (total length; mm) for all fish prey and the dominant prey group, Gizzard Shad (Chipps and

Garvey 2007). Quantile regressions provide multiple slopes that can be used as prediction intervals, providing a holistic picture of predator-prey size relationships (Cade and Noon 2003). Quantile regressions were tested for different slopes using ANOVA (alpha = 0.01). All analyses were conducted with Program R (R Core Team 2017).

Full stomachs were defined as any stomach containing a prey item. Percent full stomachs (number full stomachs / total stomachs sampled) and mean weight of individual diet items (reconstructed, pre-digested weights [g]) were both analyzed with ANOVA to test for differences among lakes, seasons, and saugeye sizes (all treated as fixed factors). Tukey's honest significant difference post-hoc procedure was used to determine pairwise differences for significant factors (alpha = 0.05).

Results

I obtained 2,589 saugeye stomachs yielding 1,301 full stomachs and 2,341 identifiable diet items. Recovered prey items included representatives from 18 fish species and four invertebrate orders (Table 2). Gastric lavage sampling removed all diet items from 90.4% of evaluated saugeye (47 of 52 stomachs verified as empty after lavage). Of the 9.6% of stomachs with unrecovered diet items, an average of 88.6% (SE = 3.7) of the total contents (by weight) had been effectively removed via gastric lavage; thus gastric lavage sampling removed 98.4% of the total weight (g) of diet items across all fish sampled (i.e., 90.4 + (9.6%*88.6%) = 98.4%). Mean saugeye relative weight (W_r) and population size structure (PSD, PSD-P) differed among lakes (Table 4).

Bivariate plots (Amundsen et al. 1996) revealed slight ontogenetic changes in feeding ecology of saugeye across the three size classes (Figure 1). All sizes demonstrated a specialized feeding strategy (majority of prey groups in upper portion) and narrow niche widths (i.e., a dominant prey group was evident in the upper right quadrant; Manko 2016). However, the dominant prey taxon switched from minnow-shaped fish (Inland Silverside *Menidia beryllina*, Logperch *Percina caprodes*, and Bluntnose Minnow *Pimephales notatus*; Table 2) for stock-size saugeye to Gizzard Shad for quality-size and larger saugeye. Each size class also contained a high degree of variation in prey types among individual diets (majority of prey groups in upper left quadrant; Manko 2016).

Mean proportions by weight (MW_i) of prey groups were variable among saugeye size classes, lakes, and seasons, with interactive patterns among these three factors (Figure 2; Table 5). Eigenvalues from correspondence analyses indicated among-lake factors explained relatively more variation in diet composition (0.644 – 0.877) than seasonal (0.142 – 0.263) or ontogenetic (0.341 - 0.721) factors, particularly in regard quality-size and larger saugeye (0.852 – 0.877; Table 6). However, ontogenetic variation was also important in explaining variation in diet composition, particularly in spring (0.721) and fall (0.626). Overall, Gizzard Shad dominated diets of preferred-size and larger saugeye, with crappie and invertebrates also being somewhat common in summer. Gizzard Shad also dominated diets of quality-size saugeye in spring and fall, but lepomids were the dominant prey in summer along with moderate levels of invertebrates and Gizzard Shad. Minnow-shaped fishes dominated the diets of stock-size saugeye in all seasons, with

moderate amounts of lepomids and Gizzard Shad also present. However, there were still subtle, but meaningful patterns among different combinations of saugeye size classes, lakes, and seasons.

With respect to lake-specific MW_i patterns, preferred-size and larger saugeye had relatively similar diet compositions in Lake Carl Blackwell, Lake McMurtry, Thunderbird Reservoir, and Lake Jean Neustadt (greater use of Gizzard Shad and crappie) and relatively different diet compositions in Lake Lawtonka (more lepomids, invertebrates, and Freshwater Drum) and Sooner Lake (more Moronids and Largemouth Bass). Likewise, quality-size saugeye had similar diets in Lake Carl Blackwell, Lake McMurtry, and Thunderbird Reservoir (relatively greater use of Gizzard Shad and crappie) whereas quality-size saugeye from Sooner Lake had greater use of Moronids and Lake Lawtonka had greater use of minnow-shaped fishes, lepomids, and invertebrates (Figure 2b). Stock-size saugeye diet compositions were relatively variable among lakes (Figure 2c).

Seasonal factors were not as strongly correlated with diet changes as lake-to-lake factors described above, but were still relatively important. Saugeye that were preferred-size or larger ate predominantly Gizzard Shad in all seasons but also ate more Freshwater Drum and fewer crappie or lepomids in spring, more invertebrates and fewer Gizzard Shad in summer, and more crappie and fewer moronids in fall (Figure 2d, Table 5). Quality-size saugeye had a more diverse diet in summer, when they ate more lepomids, invertebrates,

and crappie relative to other seasons, and ate relatively more Gizzard Shad and fewer lepomids in spring and fall (Figure 2e). Stock-size saugeye ate relatively smaller, minnow-shaped fishes in spring and fall and more moronids and lepomids in summer (Figure 2f).

Size-specific patterns in MW_i of prey groups also existed, indicating ontogenetic changes in diet composition after switching to piscivory (Table 5). Stock-size saugeye ate more minnow-shaped fishes relative to other saugeye sizes in all seasons; the use of lepomids was also higher than other saugeye size classes in spring and fall (Figures 2g-i), and the use of invertebrates was typically lower than other saugeye size classes, especially in summer (Figure 2i). Quality-size saugeye ate more Moronids in all seasons and more invertebrates in spring relative to other saugeye sizes (Figure 2i), and preferred-size and larger saugeye ate more Gizzard Shad in the spring and summer (Figures 2g, 2h). Preferred-size and larger saugeye also ate more crappie and Freshwater Drum in all seasons.

Mean percent full stomachs were 53.0% for preferred plus, 43.7% for quality, and 45.3% for stock saugeye across all seasons and lakes (Table 7). Additionally, percent full stomachs was higher in fall than spring ($F_{2,33} = 4.68$, $P = 0.03$) or summer ($F_{2,33} = 4.68$, $P = 0.04$), but no significant differences in percent full stomachs were found among lakes ($F_{4,33} = 2.04$, $P = 0.11$) or saugeye sizes ($F_{2,33} = 2.10$, $P = 0.14$). Mean reconstructed weight of individual diet items was 31.7 g (2.1% [sd = 1.6%] of saugeye weight) for

preferred-size and larger saugeye, 8.7 g (1.4% [sd = 1.8%] of saugeye weight) for quality-size saugeye, and 2.3 g (1.2% [sd = 1.8%] of saugeye weight) for stock-size saugeye across all lakes and seasons. All sizes of saugeye ate smaller prey items during summer than in spring ($F_{2,33} = 13.33$, $P < 0.01$) or fall ($F_{2,33} = 13.33$, $P < 0.01$), and larger saugeye ate larger prey items than smaller saugeye ($F_{2,33} = 51.04$, $P < 0.01$). Sooner Lake saugeye also ate smaller prey items than saugeye in Jean Neustadt ($F_{4,33} = 3.36$, $P = 0.03$) and McMurtry ($F_{4,33} = 3.36$, $P = 0.03$).

Size of all fish prey and size of Gizzard Shad found in diets increased with saugeye total length (Figure 3). Trend lines estimating the 5th percentile, median, and 95th percentile of all fish prey sizes consumed were significantly greater than zero ($P < 0.01$, Table 8), but the slope of the 5th percentile was significantly less than the slope of the median (0.50; $F = 175.32$, $P < 0.01$) or 95th percentile (0.95; $F = 127.60$, $P < 0.01$). All three Gizzard Shad prey-size slopes were significantly greater than zero ($P < 0.01$) but were not significantly different from each other. Maximum fish prey length (proportion of saugeye total length) was relatively constant across saugeye sizes (approximately 36% – 37%; Figure 4), and median fish prey length increased as saugeye grew larger (approximately 13% to 29%). Additionally, maximum Gizzard Shad prey length decreased as saugeye grew larger (approximately 45% - 36%; Figure 4), and median Gizzard Shad prey length decreased slightly as saugeye grew larger (approximately 30% - 28%).

Discussion

Saugeye had distinctly different diets among some lakes, with these lake-to-lake differences being the largest source of saugeye diet variation. This lake-specific variation suggests saugeye had differing effects on prey across systems leading to diverse top-down influences. In general, saugeye had a specialized feeding strategy and ontogenetic shift from minnow-shaped fishes to Gizzard Shad, but saugeye displayed flexibility in feeding habits and apparently adapted to different prey communities by adjusting their diets, similar to Walleye and Northern Pike *Esox Lucius* (Beaudoin et al. 1999; Pothoven et al. 2017). This flexibility in saugeye diets has several important implications. First, saugeye diet flexibility may be advantageous to reservoir food webs, potentially resulting in less interspecific competition when saugeye are introduced, if saugeye change dominant prey types when competition with other piscivores exists, although this has yet to be formally tested. Second, lake-to-lake variation in saugeye diets may also cause variable responses of White Crappie populations to saugeye stockings in systems where saugeye have been stocked as a predatory-control to combat slow-growing crappie populations (Boxrucker 2002; Galinat et al. 2002). Specifically, in lakes where saugeye do not eat large proportions of crappie (e.g., Lawtonka, Sooner), saugeye stockings will not be an effective crappie management strategy. Lastly, these diet data can be used in models (e.g., bioenergetics, Ecopath, etc.) for other southern reservoirs to account for lake-to-lake variability rather than results reported from single-lake studies, allowing models to better reflect the true range of effects saugeye might have in a new system.

Though more subtle, seasonal changes in saugeye diets appear to have important energetic consequences. Saugeye had higher proportions of full stomachs in fall compared to other seasons, likely indicating higher feeding rates and growth as gonad development begins and saugeye prepare for lower temperatures and food availability associated with winter (Malison et al. 1990). Saugeye ate significantly smaller prey, relatively more invertebrates, and had a more diverse diet (less dependence on dominant prey species) in the summer. There was also greater variation in diet among saugeye size classes in summer. These summer feeding characteristics may be explained by optimal foraging theory (Townsend and Winfield 1985). Saugeye in southern reservoirs may become more opportunistic in prey selection (including less energetically-valuable prey types if they are easier to capture) in warmer temperatures (where they may be habitat limited to cooler areas of a reservoir) and exhibit more active and targeted feeding (using more energy to target high-calorie prey species) in cooler seasons. Under optimal conditions, piscivores often select shallow- or soft-bodied prey over deeper-bodied or spinney prey (Lewis et al. 1961; Hoyle and Keast 1987b), presumably due to shorter handling time, leading to better energy efficiency for these prey types (Hoyle and Keast 1987b). My results are consistent with these patterns suggesting minnow-shaped prey and Gizzard Shad prey are associated with seasons that have optimal temperatures (i.e., spring and fall) and lakes where saugeye had more frequent use of these prey types tended to have higher saugeye condition. For example, in Thunderbird Reservoir, stock-size saugeye ate more minnow-shaped fishes (mainly Inland Silverside) and had higher relative weights than saugeye in the other lakes. Conversely, in Lawtonka and Sooner Lakes, quality-size and preferred-size and larger saugeye ate less Gizzard Shad than other

lakes and had lower mean relative weights. Similarly, saugeye in Ohio had higher growth rates in a lake with highest diet proportions of Gizzard Shad (Denlinger et al. 2006). This suggests that although saugeye are adaptable and will eat other prey types in some systems, this may come at an energetic cost that hurts condition, and possibly growth.

Oklahoma saugeye routinely consumed larger prey than most other piscivores including Walleye (Mittelbach and Persson 1998) and even saugeye in northern (Ohio) systems (Denlinger et al. 2006), which may produce stronger top-down forces than predators that eat abundant, young-of-year prey. Small (age-0) cohorts are naturally abundant to account for high losses from natural mortality. However, older cohorts already have had their abundance reduced such that a similar amount of predation mortality can have a greater overall effect at the population level. For example, focused predation on age-1 White Crappie by saugeye can result in large changes in crappie population biomass and density-dependent growth rates, even though White Crappie are not the dominant prey type for these saugeye (Chapter 4). Therefore, caution should be used when stocking saugeye in southern systems as they could have large effects than expected on their dominant prey species.

Gaeta et al. (2018) looked at predator-prey size relationships (proportions of prey length vs. predator length) for several freshwater piscivores, but did not include hybrid saugeye. My results suggest saugeye predator-prey size relationships were unusual among

piscivores according to findings of Gaeta (2018). Most predators, including Walleye, eat predominantly small prey and the prey size, as a proportion of predator length, tends to decline for larger predators (20% of predator length for smaller fish declining to 10 or 15% of predator length for larger predators; Gaeta 2018). However, saugeye reflected patterns similar to Muskellunge *Esox masquinongy*, where median prey lengths were constantly large or increased as saugeye grew larger (20-30% of saugeye length; Gaeta et al. 2018). This finding could be caused by different habitat characteristics of southern reservoirs relative to northern lakes. For example, southern reservoirs are generally turbid systems (study lakes had mean secchi depth 70.4 cm in spring, 59.4 cm in fall; Oklahoma Department of Wildlife Conservation, unpublished data). Selectivity of larger prey can be higher with increasing turbidity (Jönsson et al. 2013), thus high turbidity may drive selection of larger prey by saugeye and cause different trophic dynamics for visual predators in southern reservoirs (Carter et al. 2010).

In this study, I observed considerable differences in saugeye diets among lakes which suggests saugeye have different influences on lake-specific prey assemblages. Saugeye regularly ate larger prey than most piscivores in the literature, which could potentially cause disproportionately large effects on prey assemblages relative to other piscivores. Seasonal variation in saugeye feeding ecology appeared to influence saugeye energetics, suggesting saugeye may not grow as well in systems lacking adequate prey assemblages during summer. Therefore, it appears differences in habitat (e.g., temperature, turbidity, etc.), prey availability (e.g., less overwinter Gizzard Shad mortality, different prey assemblages, etc.), and growth rates (influencing the number of larger saugeye present in

the population) probably cause differences in saugeye feeding ecology among southern reservoirs. Researchers and managers should be aware of these dynamics when attempting to evaluate or predict the effects of introducing saugeye on lower trophic levels.

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Table 1. Name, abbreviation (Abbr.), surface area (hectares), relative location, and year sampled for six reservoirs sampled for this study. All reservoirs were sampled for one year between summer 2015 and summer 2017.

Reservoir	Abbr.	Hectares	Location	Seasons Sampled
Lake Carl Blackwell	CB	1356	North Central OK	Summer 2016 - Spring 2017
Lake Jean Neustadt	JN	187	South Central OK	Fall 2016 - Summer 2017
Lake Lawtonka	LT	970	Southwest OK	Fall 2016 - Summer 2017
Lake McMurtry	MC	467	North Central OK	Summer 2016 - Spring 2017
Sooner Lake	SO	2185	North Central OK	Summer 2015 - Spring 2016
Thunderbird Reservoir	TB	2165	Central OK	Fall 2016 - Summer 2017

Table 2. Nine prey groupings used in diet analyses of saugeye in Oklahoma reservoirs. Prey groupings were based on both taxonomic and ecological similarities shared by prey. Prey species with an asterisk composed greater than 90% (by number) of the prey group.

Prey Group	Abbreviation	Taxa
Gizzard Shad	GZS	*Dorosoma cepedianum**
		Dorosoma petenense
Crappie	CRAP	*Pomoxis annularis**
		Pomoxis nigromaculatus
Lepomid	LEP	*Lepomis macrochirus**
		Lepomis cyanellus
		Lepomis megalotis
Minnow-shaped fishes	SSLOG	*Menidia beryllina**
		Percina caprodes
		Pimephales notatus
Freshwater Drum	DRUM	*Aplodinotus grunniens*
Largemouth Bass	LMB	*Micropterus salmoides*
		Micropterus punctulatus
Moronid	MOR	*Morone americana**
		Morone chrysops
Other Fish	OTH	*Ictalurus punctatus*
		Pylodictis olivaris
		Sander vitreum X Sander canadense
Invertebrate	INV	Ephemeroptera
		Odonata
		Diptera
		Decapoda

Table 3. Coefficients for linear models used to reconstruct pre-digested total lengths of fish prey from backbone lengths (derived from completely intact prey items) and geometric means of length-weight coefficients (b and a') gathered from FishBase and the corresponding sample size (FB N; filtered to Southern populations when possible; Froese and Pauly 2017). Length-weight coefficients for Inland Silverside and Logperch were derived from intact prey items because there were insufficient records in FishBase for these species. Backbone lengths were measured from posterior edge of skull to the posterior edge of the last caudal vertebra and used to make linear relationships with total lengths of intact fish prey diet items. All coefficients of determination (R^2) were $\geq$ 0.967 for total length models.

	Total Length Coef.			Length-Weight Coef.		
Taxon	Slope	Intercept	R2	b	a'	FB N
Gizzard Shad	1.491	4.605	0.991	2.960	-1.959	3
Crappie	1.494	12.216	0.967	3.180	-2.119	30
Lepomid	1.502	0.058	0.999	3.180	-1.910	35
Inland Silverside	1.402	3.857	0.986	2.558	-4.617	N/A
Logperch	1.434	-2.693	0.993	3.174	-5.592	N/A
Freshwater Drum	1.620	-1.202	0.993	3.100	-2.316	1
Largemouth Bass	1.483	7.782	0.998	3.140	-2.060	47
Moronid	1.630	-1.767	0.996	3.120	-2.051	3

Table 4. Means and standard deviations (SD) of relative weights (W_r) for preferred-size and larger (>460 mm), quality-size (350 – 459 mm), and stock-size (200 – 349 mm) saugeye as well as PSD and PSD-P with lower and upper 95% confidence intervals (LCI and UCI, respectively) from electrofishing samples (all seasons combined) at six study lakes sampled from 2015 – 2017 (Lake Carl Blackwell [CB], Lake Jean Neustadt [JN], Lake Lawtonka [LT], Lake McMurtry [MC], Sooner Lake [SO], and Thunderbird Reservoir [TB]).

	Pref. Plus Wr		Quality Wr		Stock Wr		PSD			PSD-P		
Lake	Mean	SD	Mean	SD	Mean	SD	PSD	LCI	UCI	PSD-P	LCI	UCI
CB	89.3	12.9	86.7	11.0	83.8	23.5	69	62	75	39	32	46
JN	89.3	7.8	85.7	6.1	87.1	15.6	65	57	73	59	51	68
LT	86.5	9.9	83.1	8.5	77.7	1.5	98	96	100	47	39	55
MC	86.4	12.2	86.0	9.7	82.4	10.2	36	29	44	21	5	27
SO	75.4	27.7	83.4	21.6	94.9	28.7	59	51	68	7	3	12
TB	95.6	11.1	95.9	36.8	98.2	11.5	61	56	66	49	44	55

Table 5. Mean proportion by weight (M; average of prey group weight / total weight of diet items for each full stomach) and standard errors (SE) of nine prey groups (abbreviations defined in Table 2) consumed by preferred-size and larger (>460 mm; Preferred +), quality-size (350 – 459 mm), and stock-size (200 – 349 mm) saugeye sampled in three seasons (delineated by surface water temperatures; details in methods) from 2015 – 2017. Diet proportions from each lake were combined (All Lakes Combined) as well as partitioned into the six Oklahoma study lakes (Lake Carl Blackwell [CB], Lake Jean Neustadt [JN], Lake Lawtonka [LT], Lake McMurtry [MC], Sooner Lake [SO], and Thunderbird Reservoir [TB]). Missing values indicate the given prey group did not occur in the sample. Only prey groups that were sampled within a given lake are included. Prey taxa abbreviations are Gizzard Shad (GZS), Crappie (CRAP), Lepomid (LEP), Minnow-shaped fishes (SSLOG), Freshwater Drum (DRUM), Largemouth Bass (LMB), Moronid (MOR), Other fish (OTH), and Invertebrate (INV).

	Mean Proportion by Weight																	
	Preferred + (> 460 mm)						Quality (350 - 459 mm)						Stock (200 - 349 mm)					
	Spring		Summer		Fall		Spring		Summer		Fall		Spring		Summer		Fall	
Prey Group	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
All Lakes Combined																		
GZS	72.2	2.8	40.3	5.4	62.6	2.8	63.9	6.9	20.9	3.6	71.6	4.3	11.9	4.0	18.6	4.0	17.2	2.2
CRAP	7.8	1.7	19.9	4.4	21.3	2.4	2.0	2.0	3.9	1.7	1.0	1.0	1.5	1.5	2.1	1.5	1.1	0.6
LEP	5.8	1.5	8.7	3.0	7.9	1.6	7.1	3.5	30.4	4.0	8.9	2.7	13.8	4.2	26.4	4.4	14.3	2.1
SSLOG	1.6	0.8	2.7	1.7	1.2	0.6	2.9	2.2	8.9	2.4	8.0	2.5	68.3	5.7	34.7	4.7	64	2.9
DRUM	6.3	1.5	3.6	2.1	4.5	1.3			2.3	1.3	1.8	1.3			2.0	1.4	0.4	0.3
LMB	0.7	0.5			2.2	0.8			2.0	1.2	1.0	1.0	1.5	1.5	1.7	1.2	1.1	0.6
MOR	1.7	0.8	3.6	2.1			14.0	5.0	11.8	2.8	7.6	2.5			11.6	3.3	1.1	0.6
OTH			1.2	1.2	0.4	0.4			0.8	0.8							0.4	0.4
INV	3.9	1.2	20.0	4.4			10.1	4.3	18.9	3.4	0.3	0.3	3.0	2.1	3.0	1.6	0.4	0.4
Lake Carl Blackwell																		
GZS	89.1	4.0			56.9	9.5	91.3	6.0	10.0	6.9	81.3	10.1	36.4	15.2			27.3	7.5
CRAP	2.3	1.8	11.1	11.1	15.2	7.1	4.3	4.3	5.0	5.0								
LEP	3.4	2.4	33.3	16.7	12.5	6.1			59.2	10.7	7.4	6.3	27.3	14.1	72.4	10.2	44.8	8.3
SSLOG									2.5	2.5			27.3	14.1	24.3	9.0	22.3	6.9
DRUM	5.2	2.9	11.1	11.1	15.4	7.2			5.0	5.0	11.3	7.8					2.8	2.4
LMB													9.1	9.1				
OTH									5.0	5.0							2.8	2.8
INV	0.0	0.0	44.4	17.6			4.3	4.3	13.3	7.4					3.3	3.3		
Lake Jean Neustadt																		
GZS	73.7	6.1	80.4	8.2	54.0	5.8			74.4	17.3			12.5	8.5	10.5	6.0		
CRAP	23.0	5.9	15.2	7.3	30.7	5.4									4.0	4.0	6.3	6.3
LEP	2.0	2.0	4.3	4.3	15.2	4.1							14.1	8.5	9.6	5.6	43.8	12.8
SSLOG									9.0	9.0			73.4	11.1	65.4	9.5	50.0	12.9
LMB	1.3	1.3													2.4	2.4		
MOR															4.0	4.0		
INV			0.2	0.1					16.7	16.7					4.1	4.0		
Lake Lawtonka																		
GZS	37.2	7.4	17.4	9.4	11.8	8.1	16.7	16.7	2.0	2.0	43.0	11.1						
CRAP	0.8	0.8			5.9	5.9												
LEP	23.6	6.4	14.7	8.3	23.5	10.6	9.3	9.3	47.6	7.0	33.7	10.3						
SSLOG	2.4	2.4					24.0	16.8	11.3	4.4	18.2	8.5						
DRUM	14.6	5.2			47.1	12.5												
LMB					5.9	5.9					5.0	5.0						
OTH					5.9	5.9												
MOR	4.8	3.3																
INV	16.7	5.8	67.9	11.2			50.0	22.4	39.1	6.7								
Lake McMurtry																		
GZS	84.4	5.3	42.8	20.2	86.7	9.1	90.6	9.1	53.8	14.4	95.4	4.6	25.0	16.4	20.0	7.4	20.6	6.0
CRAP	8.0	3.9	28.6	18.4	10.1	7.3			15.4	10.4					3.3	3.3	4.4	3.1
LEP			10.8	10.7			9.1	9.1	15.5	10.4			50.0	18.9	39.3	8.9	26.9	6.1
SSLOG			3.6	3.6							4.6	4.6	12.5	12.5	26.5	8.2	43.4	7.0
DRUM	2.3	2.3							7.7	7.7					6.4	4.5		
LMB					3.2	3.2											4.4	3.1
INV	5.3	3.3	14.3	14.3			0.3	0.3	7.7	7.7			12.5	12.5	4.4	3.3	0.1	0.1
Sooner Lake																		
GZS					33.3	21.1			5.4	4.4	61.9	9.0			9.1	9.1	68.6	7.7
CRAP					17.4	16.5												
LEP							11.1	11.1	5.8	4.5								
SSLOG									7.5	4.7	8.4	5.2	75.0	25.0			18.9	6.4
DRUM	40.0	24.5							4.3	4.3								
LMB	20.0	20.0			49.2	22.0			11.3	6.4								
MOR	40.0	24.5					77.8	14.7	65.6	9.7	28.6	8.3			90.9	9.1	9.4	4.7
INV							11.1	11.1			1.1	1.1	25.0	25.0			3.1	3.1
Thunderbird Reservoir																		
GZS	78.5	6.4	37.5	10.1	73.4	3.6			68.8	12.0	88.7	5.9			57.1	13.7	3.6	1.5
CRAP	4.9	3.4	41.7	10.3	20.7	3.4			12.5	8.5			3.6	3.6			0.0	0.0
LEP	2.4	2.4			2.2	1.1					4.5	4.0					2.2	1.3
SSLOG	6.9	3.9	8.5	5.8	2.4	1.2			18.8	10.1	6.8	4.7	96.4	3.6	35.7	13.3	93.5	2.0
DRUM	7.3	4.1	8.3	5.8	0.2	0.1												
LMB					1.1	0.8									7.1	7.1	0.7	0.7
OTH			4.0	4.0														

Table 6. Sum of eigenvalues from the first two dimensions (included in plots of Figure 2) of correspondence analyses exploring among-lake, seasonal, and ontogenetic variation in diet compositions (MW_i) of saugeye in Oklahoma reservoirs. Each source of variation was also refined into three grouping categories (either saugeye size or season). Saugeye size categories included preferred-size and larger (>460 mm), quality-size (350 – 459 mm), and stock-size (200 – 349 mm), and seasons included spring, summer, and fall (delineated by surface water temperatures; details in methods). Panel letters correspond with CA plots in Figure 2.

Variation	Grouping Category	Panel	Eigenvalue
Among-lake	Preferred-size and larger	A	0.877
Among-lake	Quality-size	B	0.852
Among-lake	Stock-size	C	0.644
Seasonal	Preferred-size and larger	D	0.177
Seasonal	Quality-size	E	0.263
Seasonal	Stock-size	F	0.142
Ontogenetic	Spring	G	0.721
Ontogenetic	Summer	H	0.341
Ontogenetic	Fall	I	0.626

Table 7. Percent full stomachs (number full stomachs / total stomachs sampled) and mean weight of individual diet items (g; reconstructed, pre-digested weights) for preferred-size and larger (>460 mm; Preferred Plus), quality-size (350 – 459 mm), and stock-size (200 – 349 mm) saugeye sampled in three seasons (delineated by surface water temperatures; details in methods) and six study lakes in Oklahoma (Lake Carl Blackwell [CB], Lake Jean Neustadt [JN], Lake Lawtonka [LT], Lake McMurtry [MC], Sooner Lake [SO], and Thunderbird Reservoir [TB]) from 2015 - 2017. Differing super-scripted letters indicate means from different saugeye sizes, seasons, or study reservoirs are significantly different (alpha $\leq$ 0.05).

	Percent Full Stomachs											
	Preferred Plus[a]				Quality[a]				Stock[a]			
Lake	Spr[a]	Sum[a]	Fall[b]	**Mean**	Spr[a]	Sum[a]	Fall[b]	**Mean**	Spr[a]	Sum[a]	Fall[b]	**Mean**
CB[a]	54.7	26.5	55.3	**45.5**	38.3	47.6	43.2	**43.0**	39.3	68.2	70.6	**59.4**
JN[a]	61.7	62.2	70.6	**64.8**		46.2	60.0	**53.1**	43.2	45.5	25.4	**38.0**
LT[a]	44.2	30.4	51.5	**42.0**	9.8	51.0	52.6	**37.8**			33.3	**33.3**
MC[a]	68.3	19.4	83.3	**57.0**	45.8	38.2	78.6	**54.2**	44.4	49.2	73.8	**55.8**
SO[a]	50.0	50.0	66.7	**55.6**	22.0	41.1	38.0	**33.7**	21.1	30.6	43.8	**31.8**
TB[a]	35.3	44.4	98.7	**59.5**		40.5	90.3	**65.4**	35.3	42.1	82.0	**53.1**
Mean	**52.4**	**38.8**	**71.0**	**54.1**	**29.0**	**44.1**	**60.5**	**46.4**	**36.7**	**47.1**	**54.8**	**46.7**
	Mean Weight (g) of Individual Diet Item											
	Preferred Plus[a]				Quality[b]				Stock[c]			
Lake	Spr[a]	Sum[b]	Fall[a]	**Mean**	Spr[a]	Sum[b]	Fall[a]	**Mean**	Spr[a]	Sum[b]	Fall[a]	**Mean**
CB[ab]	39.7	7.1	43.1	**38.3**	17.5	4.7	16.9	**13.5**	7.5	0.2	3.7	**2.4**
JN[a]	33.7	27.0	36.5	**34.3**		10.7	26.8	**17.4**	2.8	3.1	1.9	**2.7**
LT[ab]	36.1	3.4	31.3	**22.9**	9.4	1.6	10.8	**4.6**				
MC[a]	35.1	23.1	30.8	**32.7**	22.6	15.6	18.8	**18.9**	4.4	1.1	3.3	**2.3**
SO[b]	23.1	1.1	27.5	**15.1**	7.3	2.4	5.1	**4.4**	1.0	0.7	3.1	**2.1**
Mean	**36.1**	**11.3**	**35.7**	**31.7**	**16.1**	**3.8**	**8.7**	**8.7**	**4.0**	**1.1**	**3.2**	**2.3**

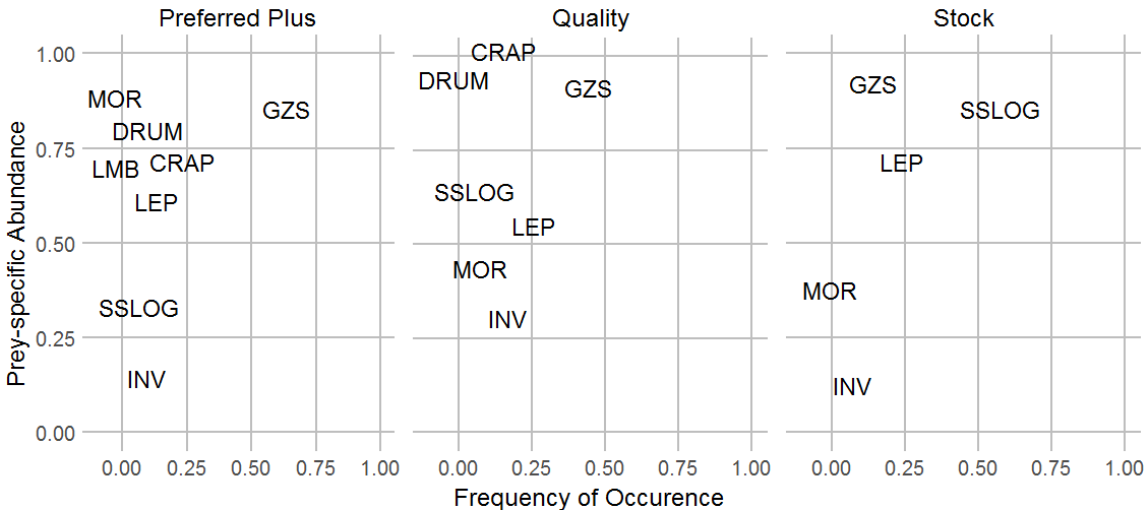

Figure 1. Bivariate plots (Amundsen et al. 1996) used to investigate prey importance, feeding strategy, and niche width of saugeye in Southern reservoirs. Only prey with greater than five total occurrences from all lakes and seasons within a given size category are included on plots. Plot axes include frequency of occurrence (total number of occurrences of a specific prey group / total number of full stomachs) and prey-specific abundance (proportion by weight; proportion that a prey group comprises of all prey items in only those saugeye stomachs in which the particular prey group occurs). Prey taxa abbreviations are Gizzard Shad (GZS), Crappie (CRAP), Lepomid (LEP), Minnow-shaped fishes (SSLOG), Freshwater Drum (DRUM), Largemouth Bass (LMB), Moronid (MOR), and Invertebrate (INV).

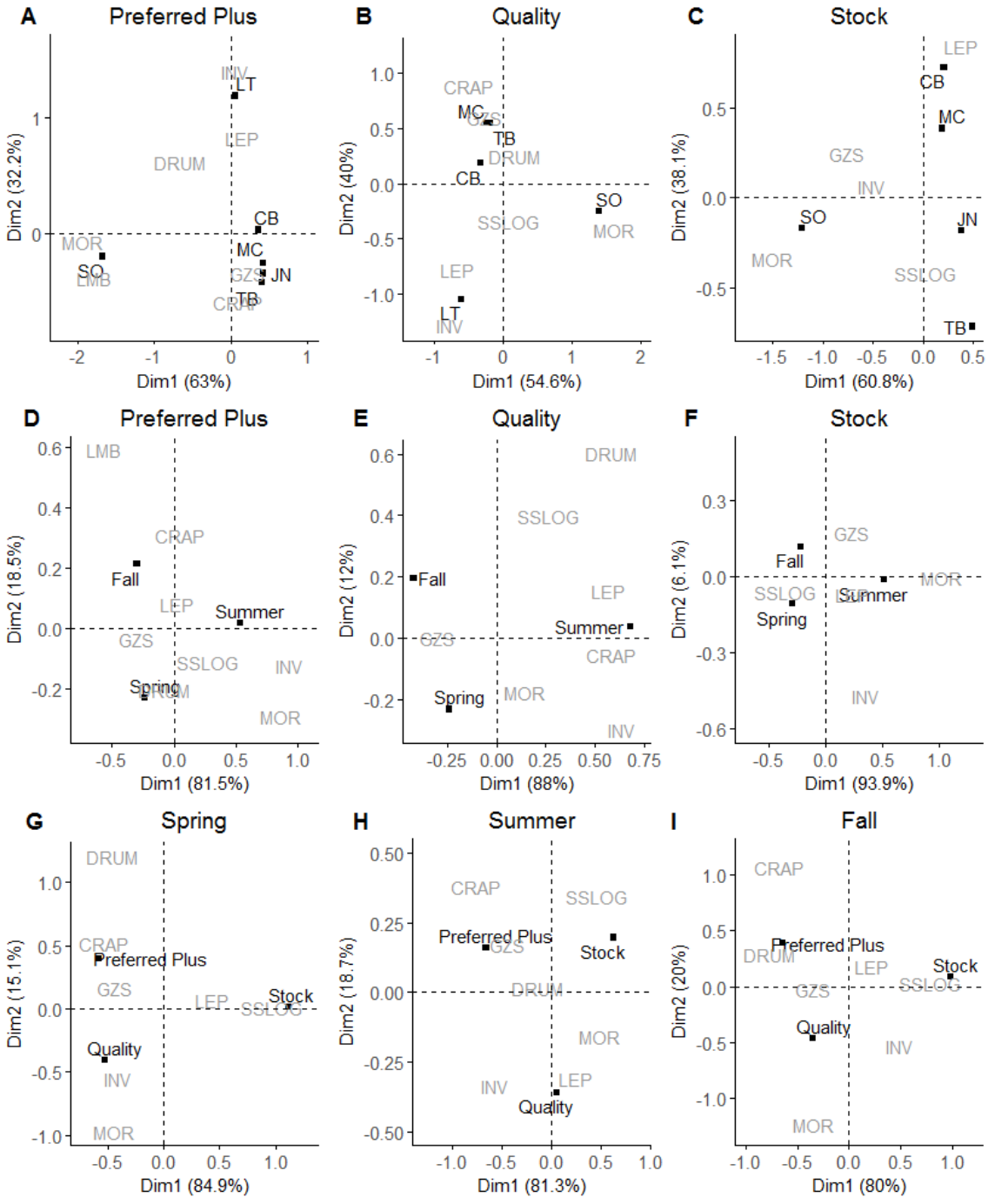

Figure 2. Correspondence analysis plots to visually assess differences in saugeye diet compositions (mean proportion by weight [MW_i]) among lakes (panels A, B, and C; grouped by saugeye PSD size category), seasons (panels D, E, and F; grouped by saugeye size category), and size category (panels G, H, and I; grouped by season). Only prey groups (Table 2) with greater than five total occurrences from all lakes and seasons within a given size category are included in plots. Prey taxa abbreviations are Gizzard Shad (GZS), Crappie (CRAP), Lepomid (LEP), Minnow-shaped fishes (SSLOG),

Freshwater Drum (DRUM), Largemouth Bass (LMB), Moronid (MOR), and Invertebrate (INV). Lake abbreviations are Lake Carl Blackwell (CB), Lake Jean Neustadt (JN), Lake Lawtonka (LT), Lake McMurtry (MC), Sooner Lake (SO), and Thunderbird Reservoir (TB).

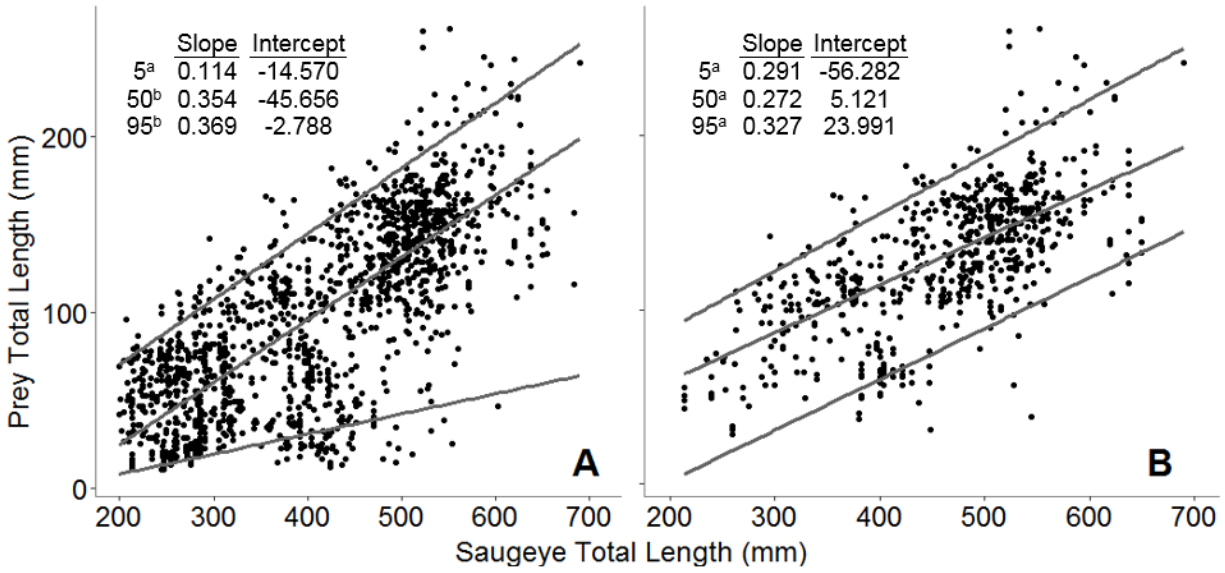

Figure 3. Quantile regressions to predict minimum (5th percentile), median (50th percentile), and maximum (95th percentile) total length for all fish prey (A; N = 1,492) and for Gizzard Shad (the dominant prey group) only (B; N = 668) from saugeye (predator) total length in Southern reservoirs. All prey total lengths are reconstructed, pre-digested total lengths. All slopes were significantly greater than zero ($P < 0.01$). Different letters indicate significantly different slopes (alpha $\leq$ 0.01).

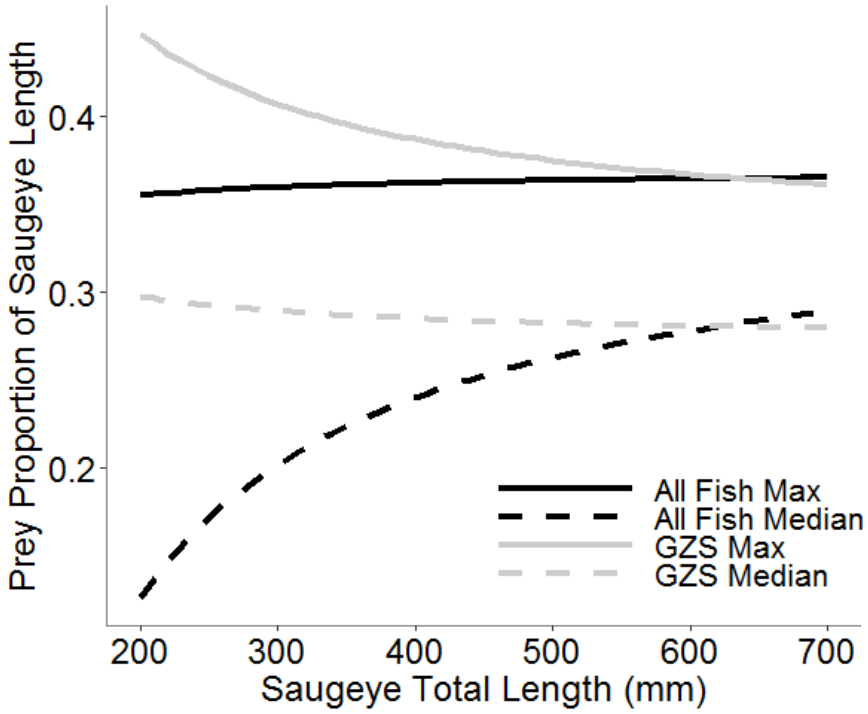

Figure 4. Trends in proportion of prey length (reconstructed total length; mm) relative to saugeye total length for median and max prey lengths (quantile regressions; 50th and 95th, respectively; Figure 3) of all fish prey and the Gizzard Shad (GZS) prey group.

CHAPTER IV

MODELING SAUGEYE PREDATION AS A BIOLOGICAL CONTROL FOR DENSE, SLOW-GROWING WHITE CRAPPIE

Introduction

Slow growth rates can lead to populations with size structure that is suboptimal for recreational anglers seeking larger fish (Isermann and Paukert 2010). These slow-growing populations can arise from changes in size-dependent survival probabilities (Ylikarjula et al. 1999; Svedäng and Hornborg 2014) or alterations in behavior and energy allocation (Jennings et al. 1997). However, growth rates are often a function of population density, where high densities of fish are associated with slow growth (Headley and Lauer 2008; Lorenzen 2008). Higher population densities can generate increased intraspecific competition for limited resources such as prey or habitat, indirectly reducing individual growth rates (Mittelbach 1988; Heath and Roff 1996). This phenomenon commonly occurs with small-bodied sportfish species and can propose problems to

fishery managers interested in improving size structure of fisheries (i.e., increasing relative abundance of larger individuals; Mitzner 1984).

Managers have attempted numerous strategies to increase size structure of important fisheries plagued by high intraspecific competition and slow growth rates. Prey stocking (Devries and Stein 1990; Hale 1996) and macrophyte removal (Cross et al. 1992) have had variable success relieving intraspecific competition and improving growth rates of sportfish. Mechanical or chemical removal of small fish within a population can be helpful, but is both time and cost inefficient and can pose negative effects on non-target species (Mitzner 1984). Populations characterized by high density and slow growth are suited for protected slot limits (Isermann and Paukert 2010) where harvest of small individuals is encouraged to reduce population density and intraspecific competition. However, this management strategy would not be successful with small-bodied sportfish (e.g. crappie *Pomoxis* spp., Yellow Perch *Perca flavescens*) because anglers do not typically harvest small fish (Isermann and Paukert 2010). Thus, increasing predator biomass as a "control" of small-bodied sportfish could be the most effective strategy to reduce densities and increase growth (Willis et al. 1984).

Predator-prey interactions are a crucial factor shaping fish communities in small, freshwater systems (Northcote 1988; Tonn et al. 1992). Increasing piscivore abundances can even lead to trophic cascades and shifts in alternative stable states in lakes (Perrow et al. 1997; Mehner et al. 2002). Predators can directly control abundances of prey

populations (Irwin et al. 2003; Weidel et al. 2007) and indirectly control growth rates and population size structure via density-dependent growth mechanisms (Guy and Willis 1990). Predatory control of prey populations has been observed with numerous piscivorous species (e.g., Hartman and Margraf 1993; Ivan et al. 2011), and management strategies aimed at increasing predator densities to manipulate prey abundances are common (Isermann and Paukert 2010).

Saugeye *Sander vitreum X Sander canadensis* is a hybrid predator and has been introduced into numerous southern reservoirs where White Crappie *Pomoxis annularis* exhibit slow growth rates (Boxrucker 2002; Boxrucker and Irwin 2002). The intention of this management strategy is to increase predator densities to decrease White Crappie population density, therefore relieving intraspecific competition and improving crappie growth and size structure. This saugeye-stocking manipulation was applied to Thunderbird Reservoir, Oklahoma (Boxrucker 2002), where it was associated with increased individual growth rates and population size structure of White Crappie. However, White Crappie population responses have been variable among other Oklahoma lakes stocked with saugeye (Chapter 2). White Crappie populations often have cyclical patterns in population structure that are stochastic or related to abiotic conditions (Mitzner 1991; Maceina 2003), making it unclear if improved White Crappie population metrics following saugeye introductions are caused by the saugeye manipulation or just coincidental to the time of the management intervention. None of the previous studies evaluating the use of saugeye to improve White Crappie growth (e.g., Chapter 2; Boxrucker 2002) directly measure the predatory effects of saugeye on

White Crappie, so it is unclear if saugeye stockings actually were able to improve White Crappie size structure. Thus, more information is needed about the mechanisms leading to the ability of saugeye introductions to improve White Crappie growth rates and population size structure before its effectiveness can be established.

Bioenergetics modeling is a tool commonly used to assess predatory effects on prey populations (Hartman and Hayward 2007) and can estimate the biomass of prey consumed by a predator population (Deslauriers et al. 2017). However, most often, results from these models ultimately end with speculation of effects on prey populations using proportions of consumed biomass vs. available biomass (e.g., Raborn et al. 2002; Irwin et al. 2003; Denlinger et al. 2006; Shepherd and Maceina 2009; Madenjian et al. 2011; Walrath et al. 2015). I sought to take an additional step and integrate bioenergetics results (consumed crappie biomass) into White Crappie population models. With this extra step, I could better evaluate whether saugeye predation exerts enough additional mortality to meaningfully influence White Crappie populations and shape population characteristics, such as size structure.

The objective of this study was to model the effects of introducing saugeye predation on White Crappie biomass, growth, and size structure. I estimated a range of crappie consumption that is likely to occur by saugeye populations, using bioenergetics models with a range of saugeye population sizes, growth rates, and proportions of crappie in the diet. These outputs were integrated into a White Crappie population model as a

predation-mortality component. Results from this study will help disentangle the mechanisms underlying this predatory-control strategy and illuminate where it will be most successful.

Methods

Bioenergetics

Modeling approach

I modeled a range of saugeye consumption rates on crappie representative of southern reservoirs using a systematic, scenario-based approach by varying three bioenergetics parameters (saugeye population size, growth rate, and diet proportion of crappie; Table 1). Baseline bioenergetics parameters were collected from Lake Carl Blackwell, a mid-sized (1,356 ha), turbid, central Oklahoma reservoir that has a typical saugeye population (Oklahoma Department of Wildlife Conservation [ODWC], unpublished data). The saugeye population exhibits consistent recruitment (stocked annually at 50.4 saugeye/ha [SE = 0.4]; 38.1 – 50.8 mm) and eats a moderate amount of crappie in terms of diet proportion (Chapter 3). Saugeye populations exhibit sexually dimorphic growth (Bozek et al. 2011) and ontogenetic changes in diet composition. Thus, I modeled each sex and cohort separately in Fish Bioenergetics 4.0 (Zweifel et al. 2010; Deslauriers et al. 2017). Additionally, stock-size saugeye (230 – 349 mm; age-0 and age-1) do not eat significant amounts of crappie (Chapter 3), therefore I only modeled age-2 through age-6 cohorts.

I ran 10 individual bioenergetics models (5 cohorts of 2 sexes) in each of 18 scenarios (Table 1). Scenarios were constructed using all combinations of 1) three levels of saugeye population size (high, mean, low), 2) three levels of individual saugeye growth rates (high, mean, low), and 3) two levels of proportion of crappie in saugeye diets (high, mean; more details in Model Parameterization). Total annual consumption of crappie by the population was calculated as the sum of consumption from the 10 individual models for each scenario. Bioenergetics results (P-values, individual total annual consumption) were compared among saugeye sexes and ages using analysis of variance (ANOVA) followed by Tukey's Honest Significant Difference (Tukey's HSD) tests for multiple comparisons. All analyses were performed in Program R (FSA, Ogle 2017; R Core Team 2017).

Model parameterization

Mean population size of age-2 and older saugeye in Lake Carl Blackwell was estimated in spring 2017 using boat electrofishing (pulsed, direct current; 7.5 Smith-Root model GPP system) and a multiple-event, mark-recapture study incorporating the Schnabel estimation method (Schnabel 1938; Seber 1982). The estimated population size was used in the bioenergetics model as the medium population and the upper and lower 95% confidence intervals were used as the high and low population densities (Figure 1b; high = 3.74 kg/ha, mean = 2.57 kg/ha, low = 1.95 kg/ha). Otoliths were extracted from a subset of saugeye (Koch et al. 2017) and aged to develop an age-length key (multinomial logistic regression; nnet R package, Venables and Ripley 2002). This age-length key was then applied to the entire spring 2017 saugeye data set (654 males and 172 females; Ogle

2016). I estimated instantaneous mortality (*Z*) using a catch curve. Instantaneous mortality was converted to annual mortality (*A*), and applied to the estimated population to distribute individuals in the populations (i.e., based on the scenario's total population size) across age classes (ages 2 through 6). I also fit separate von Bertalanffy growth curves (nlstools R package, Baty et al. 2015) for male and female saugeye to establish mean growth parameters (Figure 1c). High and low growth rates were set using the upper and lower 95% confidence intervals of the mean von Bertalanffy coefficients (Figure 1c). These von Bertalanffy-estimated saugeye lengths were applied to sex-specific length-weight regressions, producing saugeye weight increments for bioenergetics inputs.

The proportion of crappie in saugeye diets (mean proportion by weight) was estimated by sampling saugeye stomach contents using gastric lavage in a seasonally-stratified (based on surface temperature) sampling regime (more details in Chapter 3). Saugeye diet compositions (mean proportion by weight) were analyzed by size categories (preferred-size and larger [>460 mm]; quality-size [350-459 mm]) and daily diet components were developed for the bioenergetics model by interpolating between seasons (Figure 1d; Deslauriers et al. 2017). For bioenergetic scenarios using a high proportion of crappie in saugeye diets, I used the mean diet proportion plus one standard error (Figure 1d). I used the same daily reservoir temperature profile (measured hourly at 1.5 meter depth in Lake Carl Blackwell from December 11, 2016 – December 10, 2017; mean of hourly temperatures) in all bioenergetics modeling scenarios (Figure 1a). Prey and predator energy densities were obtained from published studies and personal communication

(Cumminns and Wuycheck 1971; Miranda and Muncy 1991; Eggleton and Schramm 2002; Bajer and Hayward 2006; Richard Zweifel, personal communication).

White Crappie population model

Modeling approach

I modeled the effect of saugeye consumption on White Crappie population size, growth (length at age), and size structure (PSD) using the predicted biomass of White Crappie consumed from the 18 bioenergetic scenarios tested above. The model was built in Microsoft Excel and was a discrete, age-specific model with density-dependent growth and constant recruitment. The model accounted for natural mortality, angling mortality, and mortality from saugeye predation (more details below). I evaluated model predictions from 54 scenarios, using the 18 levels of predation mortality resulting from the bioenergetics scenarios tested at each of three initial White Crappie population sizes. Saugeye introductions to improve White Crappie size structure are applied to slow-growing, high-density crappie populations (Boxrucker 2002), thus I modeled the 50^{th} percentile (4.81 kg/ha), 80^{th} percentile (12.40 kg/ha), and the 90^{th} percentile (17.16 kg/ha) of observed White Crappie densities (percentiles based on 1,137 cove rotenone samples from 106 Arkansas lakes sampled from 1972 – 2008; Jason Olive, Arkansas Game and Fish Commission, unpublished data; Figure 2). Each modeling simulation began with a baseline model with no saugeye predation mortality to which predation mortality was added and the population tracked in annual time steps until a new equilibrium was

reached (generally 10 – 15 years), after which I recorded White Crappie population biomass, growth, and size structure.

Recruitment, length-weight relationship, and abundance

Although crappie often have stochastic recruitment (Allen and Miranda 1998; Maceina 2003), I simplified my model by assuming constant recruitment so the effects of saugeye predation could be evaluated without the additional variability that stochastic recruitment would produce. Recruitment was set as the number of age-0 individuals needed to balance the baseline (no predation mortality applied) population given the mortality rate and initial total population biomass desired in the scenario. Mean weight was calculated from mean length using the White Crappie standard weight equation and a $W_r = 92$ (50th percentile of relative weight from the populations used to derive the standard weight equation; Neumann and Murphy 1991). Mean weight-at-age was then multiplied by the numeric abundance of each age class to determine the total cohort biomass for the time step. These cohort-specific biomasses were then summed to determine the population biomass.

Mortalities

I incorporated three sources of mortality into the model: natural (v), fishing (u), and saugeye predation (p). Natural mortality was set at 0.15 and u was set at 0.42, which are the average values reported from a literature review (Allen and Miranda 1995). Saugeye predation mortality ratio was set separately for each scenario as [kg consumed by

saugeye for the given scenario]/[kg of total crappie biomass in the baseline model]. The model calculated abundance of each year class as a function of the corresponding survival rates related to these mortality rates:

$$N_{t+1} = N_t * S_v * (V_{ut} * S_u) * \left(V_{pt} * S_p\right) \quad (1)$$

Where N_{t+1} is the cohort size at time t+1, N_t is the cohort size at time t, S_v is the survival rate related to natural mortality (1-v), V_{ut} is a size-based vulnerability coefficient for harvest mortality (details below), S_u is the survival rate related to harvest (1-u), V_{pt} is a size-based vulnerability coefficient for predation mortality (details below), and S_p is the size-based survival rate related to predation (1-p). All mortality/survival rates were annualized rates.

The vulnerability coefficient for harvest V_{ut} was calculated as the percent of the cohort that was large enough to be harvested (260 mm, size at which White Crappie are fully recruited to voluntary harvest; Miranda and Dorr 2000) assuming a normal distribution of fish lengths around the mean length-at-age with a standard deviation set to observed Oklahoma White Crappie growth data (age-specific standard deviation of mean length-at-age from 62 Oklahoma lakes, Kurt Kuklinski, ODWC, unpublished data). Similarly, the vulnerability coefficient for saugeye predation mortality V_{pt} was calculated based on the length distribution of the cohort relative to the length distribution of White Crappie recovered from saugeye diets (Figure 3).

Density-dependent growth

Mean lengths-at-ages were modeled using the exponential decay function from Allen and Miranda (1998) based on the total population biomass in the previous time step:

$$PG = a + b * e^{-c*PD} \quad (2)$$

where *PG* is the proportion of median length-at-age, *PD* is the proportion of median density, *a* describes the lower asymptote, *b* describes the magnitude of *PG*, and *c* describes the shape of the curve. Individual density-dependent growth functions were incorporated for each of age classes 0-4 (density was only correlated with growth for ages 0-4; Figure 4). The exponential decay functions were fit using percentiles from a distribution of mean lengths-at-ages for 294 White Crappie populations of 62 Oklahoma lakes (standardized fall fyke net sampling from 294 lake-and-year combinations sampled between 1983-2012) and from a distribution of abundances (kg/ha) from 1,137 White Crappie populations of 106 Arkansas lakes (standardized summer cove rotenone samples from 1972-2008; Figure 2a). The nature of this relationship was such that the 10th percentile growth occurred when the population was at the 90th percentile of abundance and vice versa, with median growth occurring at the median population abundance. Oklahoma and Arkansas are of similar latitudes and shapes of the abundance distributions (catch-per-unit-effort [CPUE] from OK, kg/ha from AR) were also very similar (Figure 2). Mean lengths-at-ages for age-5+ classes were established by adding the mean growth increment for the age class (derived from the 294 Oklahoma White Crappie population samples above) to the mean length-at-age of the previous age class, thus allowing density-dependent growth observed through age-4 to continue to be reflected at older age classes even though the actual amount of growth for age-5+ was no longer density-dependent.

Model validation

I validated the accuracy of the models by comparing observed trends in White Crappie population dynamics from field samples at Thunderbird Reservoir, Oklahoma to my modeled changes in crappie population characteristics. Thunderbird samples were separated into periods of before (1983-1986) and after (1987-1997; model reached equilibrium in about 10 years) saugeye introduction (similar to Boxrucker 2002). I compared relative changes in abundance (percent change in CPUE [number/net night] for observed samples from Thunderbird; percent change in numeric density [number/ha] from the model), growth (mean lengths-at-ages 1 and 2 [mm]), and size structure (PSD and PSD-P) using data from Boxrucker (2002) and ODWC standardized fall fyke net samples (Kurt Kuklinski, ODWC, unpublished data). Samples from the period before saugeye stocking suggested Thunderbird White Crappie density was initially at the 95th percentile for abundance (103 fish/net night; approximately 22.0 kg/ha; Figure 2; ODWC, unpublished data). After saugeye became established in Thunderbird, they were relatively abundant (Boxrucker 2002), grew fast (mean length at age 2 = 450 mm; Leeds 1988), and had diets composed of high proportions of crappie (Leeds 1988; Chapter 3; highest of six Oklahoma reservoirs sampled). Therefore, I modeled saugeye predation with bioenergetics scenario 1 (Table 1; 1.34 kg/ha crappie consumed) as a validation for the model of saugeye predation on White Crappie population dynamics.

Results

Saugeye consumption of crappie

Bioenergetics modeling estimated that saugeye consumed between 0.17 kg/ha/yr and 1.34 kg/ha/yr of crappie (Table 1). The mean scenario (scenario 10) resulted in saugeye consuming 0.33 kg/ha/yr of crappie, but the overall mean crappie consumption from all scenarios was 0.54 kg/ha/yr. Saugeye did not consume significant amounts of crappie in the spring (Figure 5) because most of their diet in that season is Gizzard Shad *Dorosoma cepedianum* (Chapter 3). Consumption of crappie peaked in early summer and fall, when saugeye had higher proportions of crappie in their diets and temperatures were optimal for saugeye growth. Saugeye consumed less crappie during high, mid-summer water temperatures (peak > 30.0°C).

Saugeye P-values (proportion of maximum consumption C_{max}) significantly decreased with saugeye age ($F_{4,170} = 321.9$, $P < 0.01$), and female saugeye had significantly higher P-values than males (Figure 6a; $F_{1,170} = 1064.2$, $P < 0.01$). However, total annual consumption (all prey) by individual saugeye significantly increased with saugeye age ($F_{4,170} = 27.1$, $P < 0.01$), and female saugeye consumed significantly more total prey than males (Figure 6b; $F_{4,170} = 375.0$, $P < 0.01$). Age-2 and older female saugeye consumed an average of 3.22 kg of prey per year, and age-2 and older male saugeye consumed an average of 2.15 kg of prey per year.

Effects of saugeye predation on White Crappie biomass, growth, and size structure

Saugeye predation mortality considerably decreased densities of White Crappie populations at all three initial crappie densities (Figure 7a). When starting at the high (90^{th} percentile) crappie density (17.2 kg/ha), high levels of saugeye predation mortality were able to remove about 50% of initial crappie biomass. However, when starting at the lowest tested (50^{th} percentile) crappie density (4.8 kg/ha), high levels of saugeye predation mortality removed roughly 80% of initial crappie biomass, with diminishing returns in biomass removal after the addition of about 0.5 kg/ha saugeye consumption.

Saugeye predation increased mean length-at-age for age 1 and 2 White Crappie in all scenarios due to the density-dependent growth relationship in the model (Figure 7b). When initial crappie densities were set at the 50^{th} percentile, I observed diminishing returns for growth at higher saugeye consumption levels because crappie were already growing at maximal rates (Figure 7b). When initial crappie densities were set at the 80^{th} and 90^{th} percentiles, growth increased linearly across all saugeye predation levels, producing increases in White Crappie size of up to 30-40 mm and 46-61 mm for age-1 and 2 crappies, respectively (Figure 7b).

The effects of saugeye predation on White Crappie size structure were more complicated (Figure 7c). At the 50^{th} percentile initial population density, both PSD and PSD-P notably decreased after introduction of saugeye-induced mortality (Figure 7c). However, at the 80^{th} percentile initial population density (12.4 kg/ha), both PSD and PSD-P increased at low and moderate levels of saugeye consumption (maximum 8 and 12 unit

increase, respectively), before dropping again at higher levels of saugeye consumption (Figure 7c). Lastly, at truly dense initial population densities (90^{th} percentile), PSD and PSD-P increased at all levels of saugeye predation mortality (maximum 12 unit increase in each metric; Figure 7c).

Thunderbird field validation

Changes to the White Crappie population metrics before and after saugeye introduction were similar between the model and data observed in Thunderbird Reservoir (Table 2). The direction of change for all White Crappie metrics were the same in the model and Thunderbird Reservoir (abundance declined, growth and size structure increased), but the model had slightly smaller changes than what was actually observed in the reservoir for all metrics but PSD-P. (Table 2).

Discussion

Saugeye predation can shape White Crappie population characteristics by directly reducing biomass despite crappie not being the primary saugeye prey (Chapter 3; Leeds 1988). Saugeye ate relatively large fish prey (e.g., most crappie consumed were age-1 or age-2; Chapter 3) compared to what most predators eat (generally age-0 prey; Michaletz 1998; Dennerline and Van Den Avyle 2000). This produced a stronger population-level effect than had they focused on age-0 crappie, which are more abundant and typically experience high natural mortality (Allen and Miranda 1998). This may also help mediate

effects of high recruitment years (Allen and Miranda 2001), potentially enabling saugeye control of White Crappie abundance.

Saugeye predation only improved size structure of White Crappie in high-density populations due to a tradeoff in how mortality affected density-dependent growth and lifespan. Initial predation mortality reduced abundance allowing density-dependent growth to increase. This density-dependent growth improved size structure up to a point, but additional mortality also reduced the number of fish that lived long enough to reach quality or preferred size. Populations with high initial densities were able to tolerate higher mortality rates without negative effects on size structure (PSD) compared to median and lower population densities. I observed a maximum increase of approximately 12-15 PSD units as a result of stocking saugeye when initial White Crappie population density was $\geq$ 12.4 kg/ha, but PSD declined rather than improved when initial population sizes were < 9.6 kg/ha. Therefore, saugeye stockings should only be considered for slow-growing White Crappie populations that have unusually high-abundance.

The model predicted White Crappie population changes in Thunderbird Reservoir relatively well, but slightly underestimated effects for all metrics except PSD-P. Biotic interactions (i.e., predation, competition, etc.) are likely not the only factors regulating individual growth rates and recruitment of crappie populations (Mitzner 1991). For example, White Crappie populations throughout Oklahoma experienced increased growth

and size structure during the 1990's even in systems that were not stocked with saugeye (Chapter 2), indicating environmental or coarser-scale factors are also involved (e.g., precipitation, hydrology, or turbidity; Sammons and Bettoli 2000; Maceina 2003). Therefore, even though my results demonstrate that saugeye stockings can strongly alter White Crappie size structure, results will be somewhat variable among systems depending on the abiotic conditions involved.

Several assumptions and limitations of my model could limit its application to natural systems. First, White Crappie populations often demonstrate erratic or cyclic recruitment patterns (Allen and Miranda 2001; Maceina 2003), and my population model assumed constant recruitment. Assuming constant recruitment was logical because relationships between crappie recruitment and stock densities (Bunnell et al. 2006; Siepker and Michaletz 2013) or environmental variables (Maceina and Stimpert 1998; Maceina 2003) are inconsistent within the literature, and adding stochastic reproduction would only make it difficult to evaluate the effects of predation (but would still have the same average result, just with greater variability). Second, the model assumed saugeye predation mortality was additive (i.e., no compensatory mortality). This assumption is supported by the observations of Allen et al. (1998) where crappie mortality was additive at exploitation rates greater than 40%. Third, the model assumed mortality was not density-dependent. Although Allen and Miranda (1998) described density-dependent mortality for age-0 natural mortality, total mortality was not correlated with density in my dataset. Lastly, the model assumed diet composition of the saugeye population includes at least a moderate proportion of crappie ($\geq$ approximately 10% by weight for preferred

size and larger saugeye in summer and fall). This may not be the case in all systems where saugeye could be introduced, and my model results would overestimate the effects of saugeye introductions in these systems. Despite these assumptions, my model still performed well predicting White Crappie population changes in a high-density population, Thunderbird Reservoir, suggesting these assumptions were not so important as to lead to large errors.

Results from this study lead to several management recommendations for using predatory-control to improve White Crappie fisheries. The model suggests improvements in White Crappie size structure will be limited to high-density White Crappie populations. Therefore, saugeye should only be stocked for predatory control into lakes with White Crappie densities $\geq$ 9.6 kg/ha, and White Crappie size structure is improved most with light to moderate levels of saugeye consumption (i.e., < 0.5 kg/ha consumption by saugeye) in populations near 12.4 kg/ha. In White Crappie populations $\geq$ 17.2 kg/ha, higher stocking rates of saugeye may be beneficial for maximum potential of predatory control. Similarly, to produce sufficient predation pressure, preferred-size and larger saugeye diet proportions should include at least 10% crappie by weight. This will require adaptive management techniques individualized by lake (McMullin and Pert 2010), where stocking rates can be adjusted in light of diet information and saugeye growth rates to achieve the desired level of crappie consumption.

In many cases, bioenergetics estimates of predator consumption are not enough to predict effects of predators on prey populations, and further modeling is required to confidently determine population-level effects, such as in this study. Saugeye predation only increased White Crappie mortality 1.0%-7.8% across the entire crappie population for population densities at the 90th percentile. This overall mortality rate caused by saugeye appeared to be a minor factor influencing White Crappie populations. But, integrating these consumption values into a White Crappie population model accounted for size-specific mortality and density-dependent growth, showing that predation mortality could have substantial impacts on White Crappie biomass, growth, and size structure because the mortality was focused primarily on age 1-2 fish. Further, the model highlighted when this predatory-control will work best and helped illustrate the mechanisms governing the White Crappie management strategy. My analysis also demonstrates that biotic interactions can play a large role in shaping fish communities in confined systems such as lakes and reservoirs (Lampert 1987; Jackson et al. 2001). Further, this study illustrates not only the potential beneficial use of biological controls for management purposes, but also serves as a caution of the potentially strong community-level effects of introducing additional top-predator sportfish into reservoirs (Eby et al. 2006).

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Table 1. Eighteen scenarios modeled in Fish Bioenergetics 4.0 to predict annual consumption of White Crappie by saugeye populations. Scenarios were tested for all combinations of three parameters: population size (high, mean, low; Figure 1b), saugeye growth (high, mean, low; Figure 1c), and White Crappie (WHC) diet proportion (high, mean; Figure 1d). Each sex and cohort (age 2-6) of saugeye were modeled separately (10 model runs per scenario), and consumption values were added to estimate total annual consumption of crappie by the saugeye population (kg/ha).

	Saugeye Bioenergetics Paramters			WHC consumed
Scenario	Population Size	Growth	WHC Diet Prop.	(kg/ha)
1	high	high	high	1.34
2	high	high	mean	0.75
3	high	mean	high	0.90
4	high	mean	mean	0.49
5	high	low	high	0.62
6	high	low	mean	0.33
7	mean	high	high	0.92
8	mean	high	mean	0.51
9	mean	mean	high	0.62
10	mean	mean	mean	0.33
11	mean	low	high	0.42
12	mean	low	mean	0.23
13	low	high	high	0.70
14	low	high	mean	0.39
15	low	mean	high	0.47
16	low	mean	mean	0.26
17	low	low	high	0.32
18	low	low	mean	0.17

Table 2. Comparison of modeled and observed effects of saugeye introductions on White Crappie abundance, mean lengths-at-ages 1 and 2 (Age-1, Age-2), and size structure (PSD, PSD-P). Observed data were from Thunderbird Reservoir, OK. Values are the difference (negative or positive) from before to after saugeye introduction periods. Abundance was measured as percent change given different units between modeled (density, number/ha) and observed (fyke net CPUE, number/net night) values. Other metrics are in original units (mm for length-at-age, PSD units for PSD).

	Abundance	Age-1	Age-2	PSD	PSD-P
Thunderbird Observed	-69.3%	24.7	37.7	21.9	4.5
Thunderbird Modeled	-50.2%	18.6	28.9	10.5	5.9

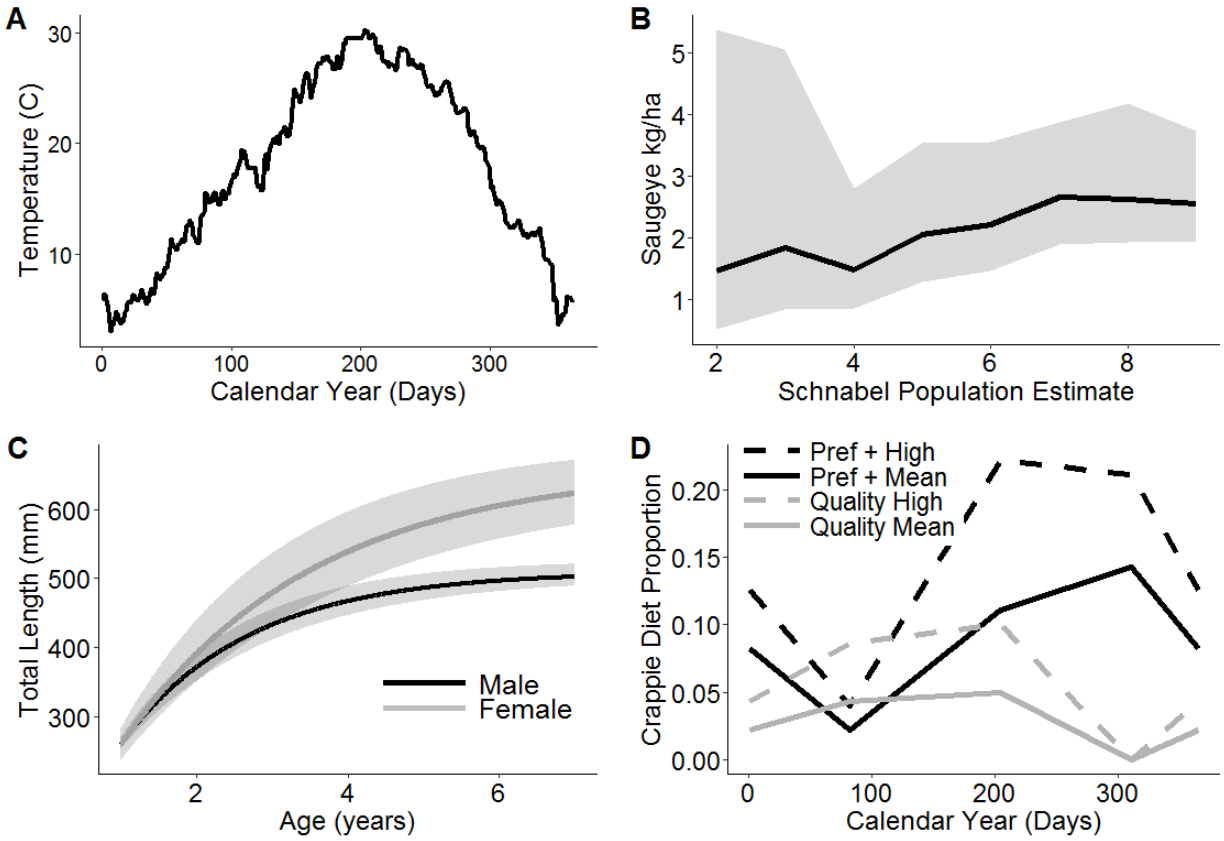

Figure 1. Baseline parameters used in bioenergetics models. Data were collected at Lake Carl Blackwell, Oklahoma and include: A) temperature profile used in all scenarios (1.5 m depth), B) Schnabel mark-recapture population size estimate of age-2 and older saugeye (upper and lower 95% confidence intervals [shaded] used for high and low population sizes), C) von Bertalanffy growth curves for both male and female saugeye (upper and lower 95% confidence intervals [shaded] used for high and low saugeye growth rates, and D) Seasonal high and mean crappie diet proportions (mean proportion by weight) for preferred-size and larger (>460 mm, Pref +) and quality-size (350 – 459 mm) saugeye (high crappie diet proportions represented by mean diet proportion plus one standard error).

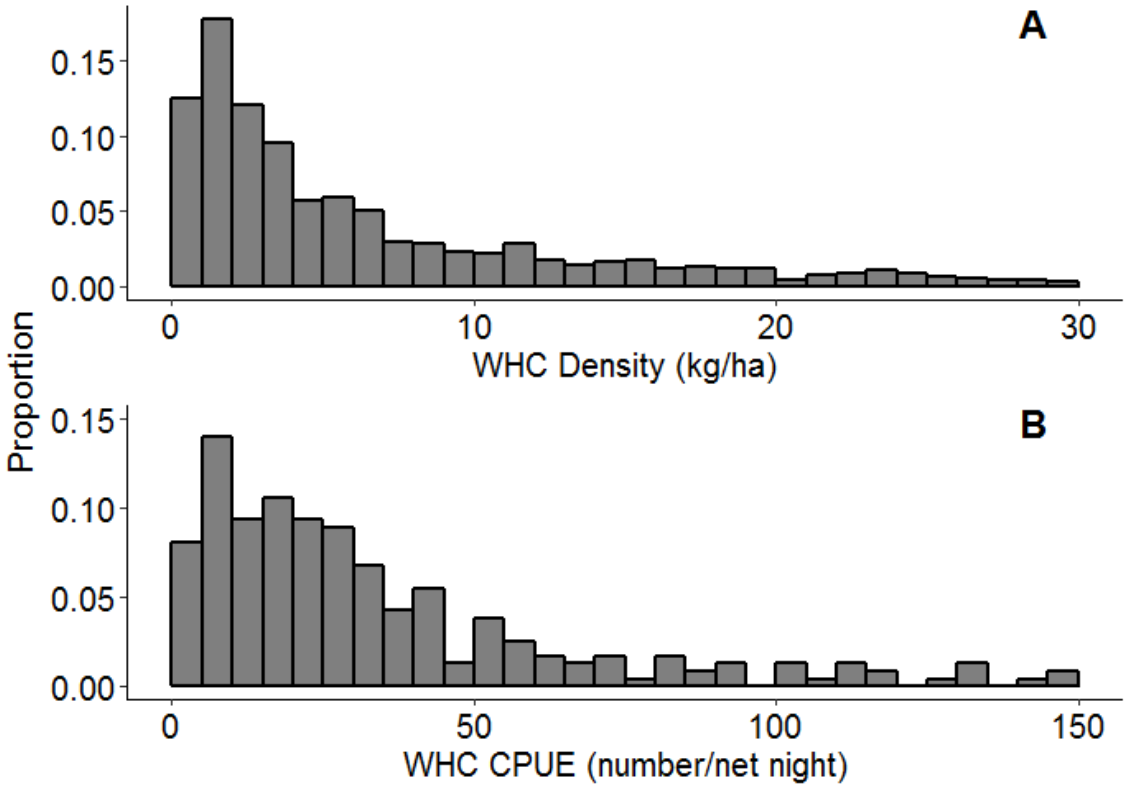

Figure 2. A) Distribution of White Crappie densities from 1,137 cove rotenone samples in 106 Arkansas lakes from 1972 - 2008. B) Distribution of White Crappie catch-per-unit-effort (CPUE; number per net night) from 294 standardized fall fyke net samples of 62 Oklahoma lakes from 1983 – 2012. I integrated White Crappie density data (A) with growth data from fyke net samples (B) to build density-dependent growth relationships in the White Crappie population model.

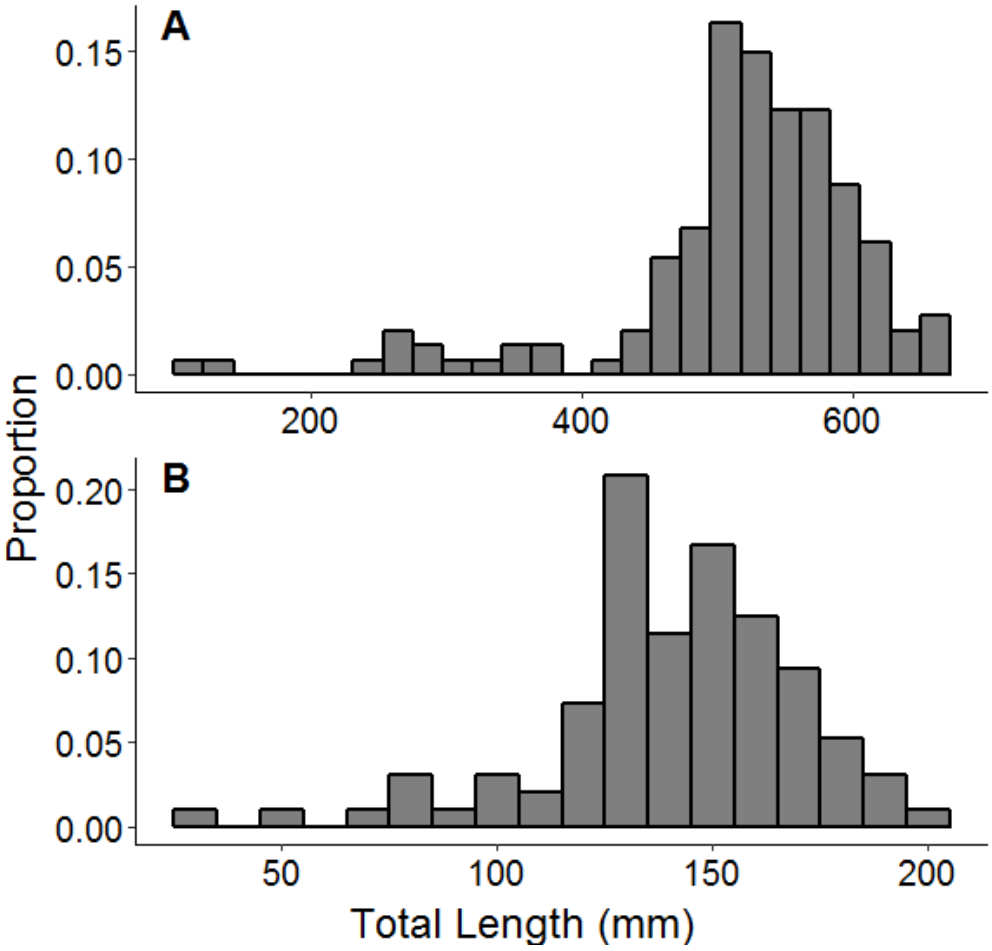

Figure 3. A) Length-frequency histogram of saugeye that consumed a crappie (N = 147) from diet samples of six Oklahoma reservoirs from 2015 - 2017. B) Length-frequency histogram of White Crappie total lengths recovered from saugeye stomachs (N = 96).

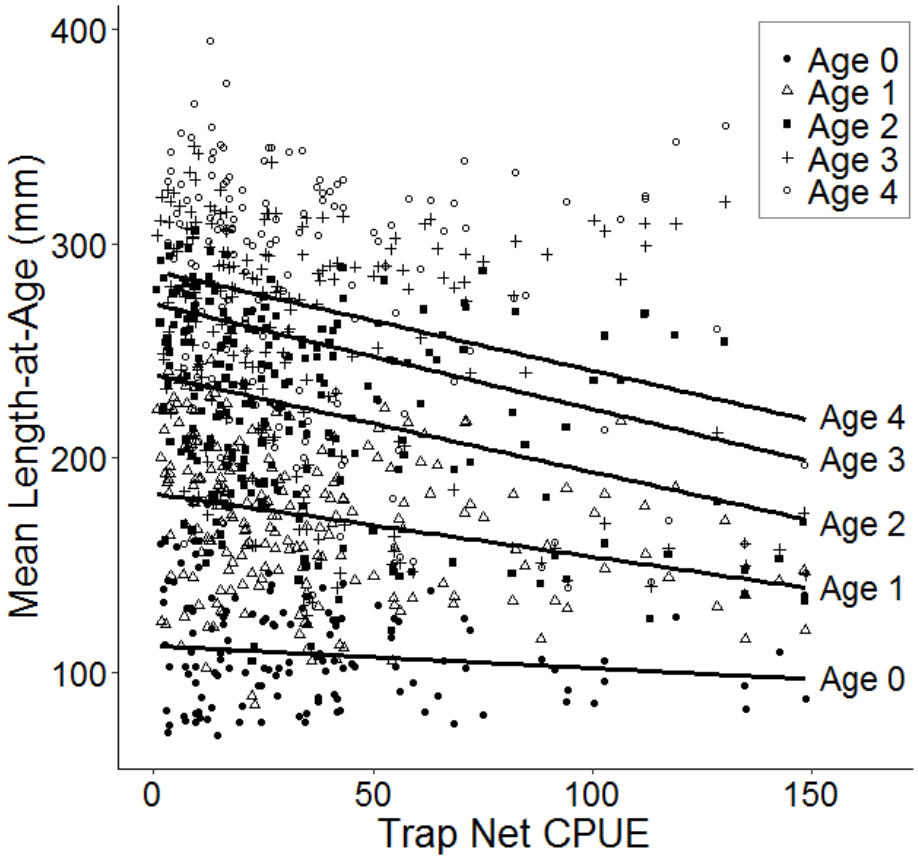

Figure 4. Age-specific patterns of density-dependent growth (mean length-at-age) for age-0 through age-4 White Crappie using catch-per-unit-effort (fall fyke net sampling; number per net night) as a proxy for population density. All age classes up to age-4 had slopes significantly less than zero ($P < 0.10$). Age-5+ fish did not have significant slopes, and are therefore not included. These growth data were used to parameterize density-dependent growth functions.

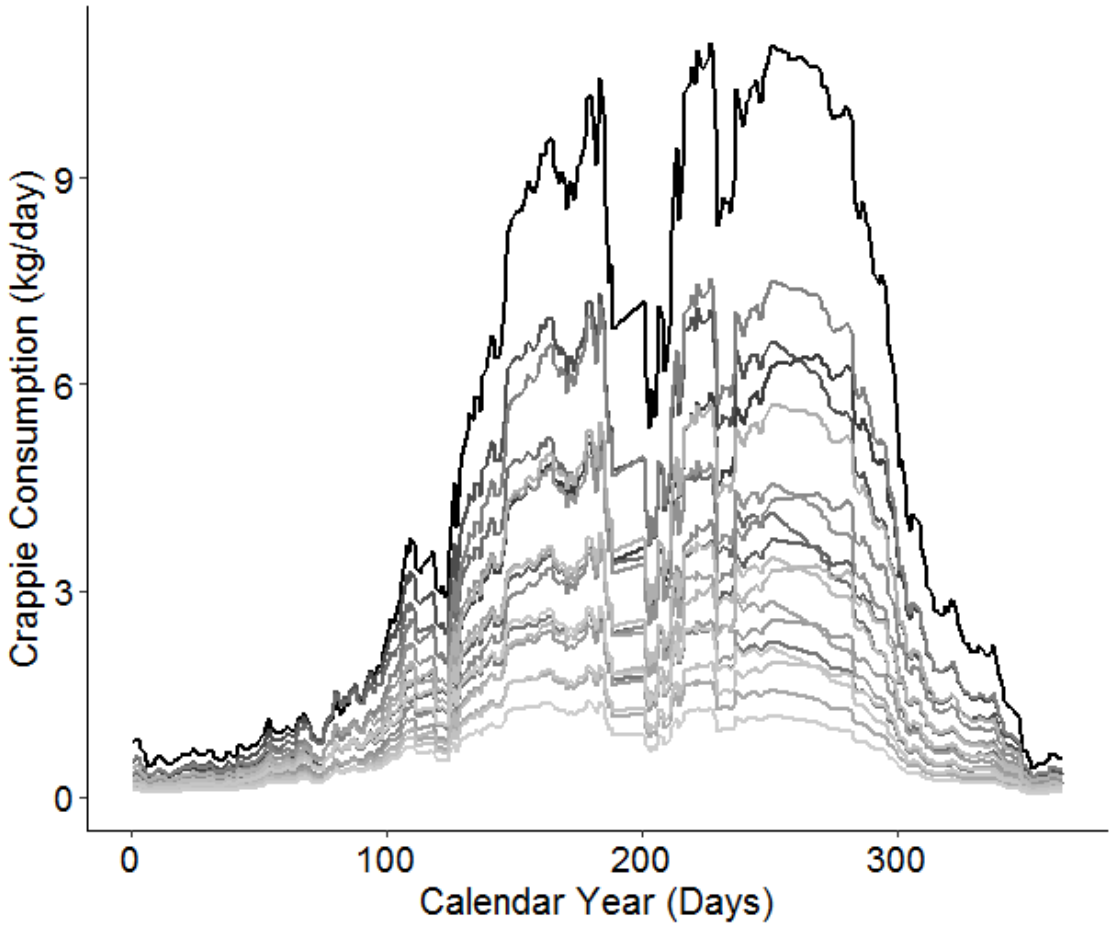

Figure 5. Daily crappie consumption (kg/day) by saugeye populations in the 18 scenarios (Table 1) modeled using bioenergetics throughout a calendar year (starting January 1). Mean crappie consumption from all scenarios was 0.54 kg/ha.

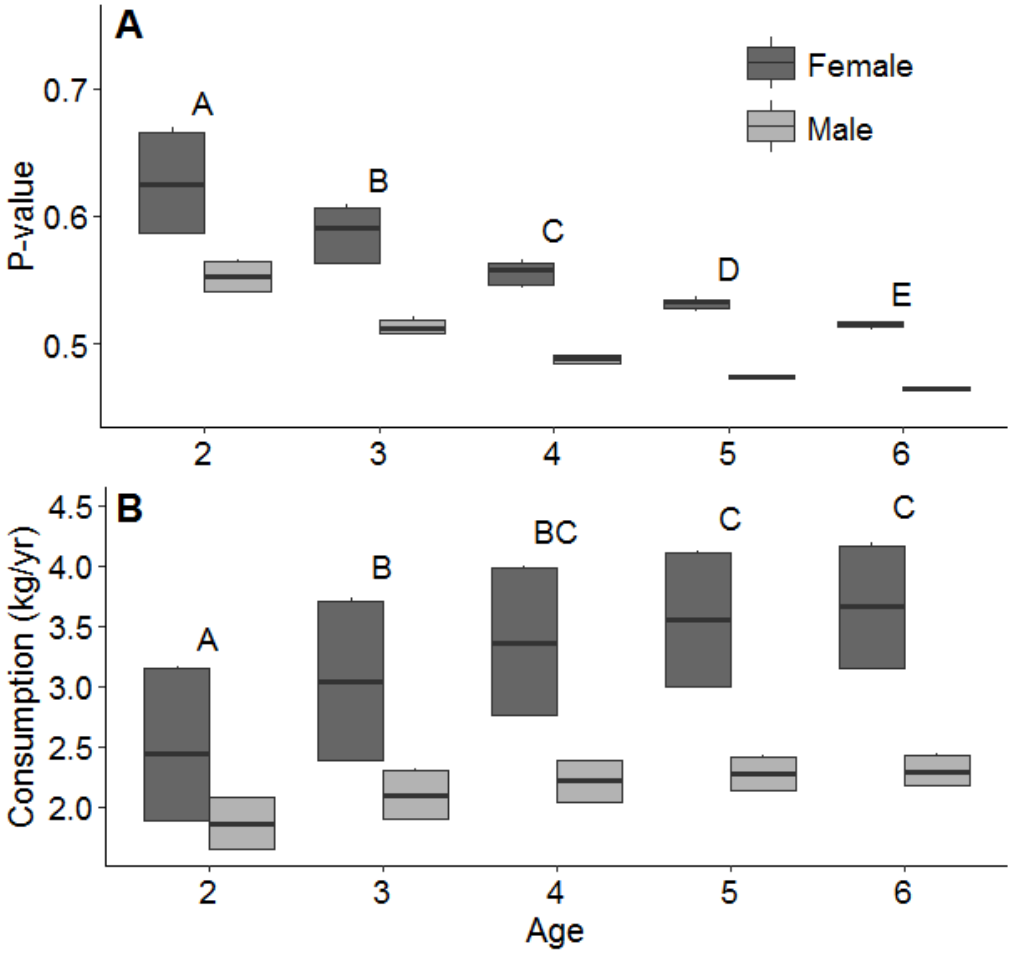

Figure 6. A) Bioenergetic P-values (proportion of max consumption [C_{max}]) and B) total annual consumption by an individual saugeye of female (dark grey) and male (light grey) saugeye from 18 modeling scenarios (varying saugeye population size, growth rate, or percent of White Crappie in the diet). Thick lines indicate medians, boxes indicate the inner-quartile range (IQR), thin horizontal lines indicate reasonable extremes (+/- 1.58 times IQR/sqrt[n]), and dots indicate outliers. Different letters indicate age classes were significantly different ($P \leq 0.05$). Males and females were significantly different in both panels.

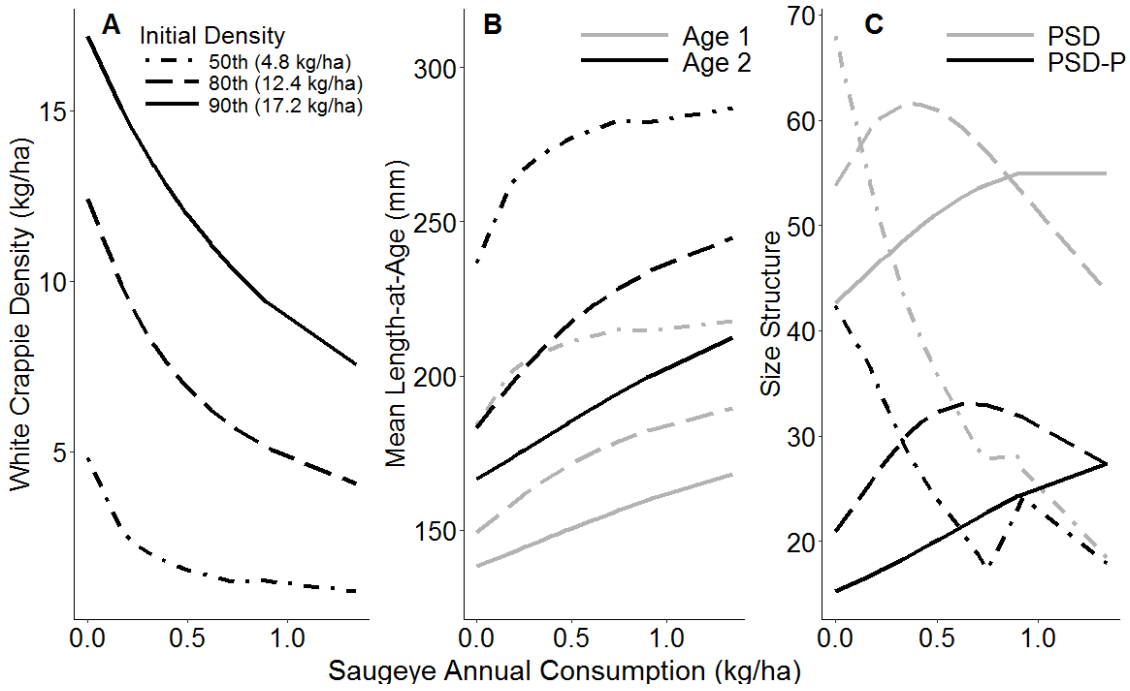

Figure 7. Effects of different levels of saugeye consumption on White Crappie A) population biomass, B) growth (mean lengths-at-ages 1 and 2), and C) size structure (PSD and PSD-P). Simulations with three different initial White Crappie densities were used: 4.8 kg/ha (50th percentile; light grey lines), 12.4 kg/ha (80th percentile; dark grey lines), and 17.2 kg/ha (90th percentile; black lines). All metrics were measured after the population model came to equilibrium.

VITA

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